"STUDIES ON SOME SENSORY STRUCTURES IN ARACHNIDS"

(Chemo and mechanoreception in the scorpion,

Heterometrus fulvipes)

By

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CONTENTS

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CHAPTER I

CHEMORECEPTORS ON THE PEDIPALPS

INTRODUCTION

Chemoreception has long been recognized as a major sensory mechanism in the feeding, reproductive, and orientation activities of many animals. Much of our present knowledge about the chemoreceptors comes from the well coordinated behavioural, histological and physiological studies on insects. By observing the responses to food, other attractants and odours, it had been established that the principal sites of chemoreceptors in insects are antennae, maxillary and labial palpi or their homologues, legs and ovipositors. Despite the extensive histological studies by Hauser (1880), Schenk (1903) and Vogel (1923b) to the present time, the identity of chemoreceptors is known in a few cases only. It is because areas supposed to be the principal sites of chemoreceptors contain large and heterogeneous population of sensilla, where the assignment of chemoreceptive function to specific sensilla had became an arduous and uncertain task (cf. Dostal 1958; Schneider 1961). Secondly the identification of chemoreceptors has probably been retarded by the tendency to assign the function of chemoreception to all sensilla whose structure conform to some postulated norm. The reviews by Forel (1908), McIndoo (1914a, 1914b), Von Frisch (1921), Minnich (1929a), Marshall (1935), Dethier and Chadwick (1948a), Dethier (1953;1963) had furnished voluminous information, ofcourse real and supposed on the structure of the chemoreceptors.

Receptors sensitive to stimulation by chemical solution applied directly had been identified positively in Diptera, Lepidoptera, Hymenoptera and Coleoptera. Frings and Frings (1949) gave an account of the location of the contact chemoreceptors in various insects and other animals. They may be the trichoid sensilla, located on the legs, and mouth parts and the sensilla basiconica situated on the labella of the flies. The studies by Grabowski and Dethier (1954), Dethier (1955a), Dethier and Wolbarsht (1956), Stürckow (1960), Dethier and Evans (1961), Mellon and Evans (1961), and Larsen (1962), furnished the structural details of the chemoreceptors in insects.

Dethier and Chadwick (1948a) enumerated the different criteria followed in the studies for locating and mapping of the contact chemoreceptors. The threshold studies revealed individual differences in a given species. Dethier and Chadwick (1947) showed that such differences in a population of Phormia were not statistically significant. From the threshold determinations the sensitivity of the response was observed to vary with the receptor field stimulated (Minnich 1931, 1932; Frings 1944; Frings and O'Neal 1946; Hodgson 1951; Dethier 1955a). Further studies revealed relationship between sensitivity and the receptor stimulated. Von Frisch (1935), Imamura (1938), Frings (1946), and Frings and O'Neal (1946), observed that insects under their study could discriminate the intenstity of a concentration range

of a compound. Employing the modern electrophysiological techniques Morita and Takeda (1959) stated that this is possible because in a chemoreceptor hair of Venessa indica, a single neuron responds only to a particular concentration range of sodium chloride.

The later studies showed that in insects the stimulative efficiency could be correlated directly with the ionic mobilities in electrolytes (Frings 1945, 1946, 1948; Frings and O'Neal 1946; Dethier 1947c, 1955a; Hodgson 1951). The behaviour of insects towards divalent ions is noticeably different from that of the monovalent ions (cf. Hodgson 1951), suggesting some possible differences in the molecular structure of the receptors as had been proposed for mammals (Beidler 1953, 1954, 1960; Beidler, Fishman and Hardiman 1955). From a comparative study of the order of acceptance of the sugars with honey bees (Von Frisch 1935), Calliphora (Haslinger 1935) and Phormia (Hassett, Dethier and Gans 1950), certain general relationships were established and were reviewed by Detheir (1955a). Hodgson (1958b), Case and Gwilliams (1961) and Case (1964) reported the presence of receptors in crayfish and crabs sensitive to amino acids, especially glutamic acid. Laverack (1963) found that only trimethyl amine oxide (TMO) and betain to be consistantly stimulatory in related species.

But it was not until the discovery and the successful application of the modern electrophysiological techniques

that the recording of action potentials from the chemoreceptive hairs, an understanding of the categories of the different receptors and a grasp of the mechanism of action of the receptors was made possible. After repeated trials and failures in recording action potentials by standard techniques Hodgson, Lettvin and Roeder (1955), Morita, Doira, Takeda and Kuwabara (1957) independently developed a novel electrophysiological technique. Recently a greatly improved technique was developed by Morita (1959). From the different potentials recorded from the chemoreceptor hairs of Phormia five neurons were distinguished, one of which designated as 'L' fibre responding for salts, the second as 'S' fibre responding for sugars (Hodgson and Roeder 1956), the third neuron designated as 'M' (mechanoreceptor) responding for bending of the hair (Wolbarsht and Dethier 1958). Mellon and Evans (1961) detected the fourth neuron which responds to water. Stürckow (1960) reported the presence of a fifth neuron in some hairs but could not assign any function. A peripheral discriminatory mechanism for the stimulating compounds has been studied electrophysiologically in several species of insects (Hodgson 1957, 1958b; Morita and Yamashita 1959: Stürckow 1959, 1960; Takeda 1961; Evans and Mellon 1962; Brown and Hodgson 1962).

It is in the light of these discoveries that the chemoreceptors among insects are known to be highly specialized and specific. Perhaps the same reason prompted Dethier (1962) to assign a more meaningful division for the chemorecep-

tors as salt, sugar or sex attractant receptors than of olfactory and contact chemoreceptors. However, in the absence of a substantial knowledge of their physiology he prefers the retention of the same ambiguous division still to be convenient.

The foregone account showed that most of the studies were confined only to the insects and very little attention was paid to arachnids which comprises animals with diverse habits and habitats. From the available literature it is obvious that some attention had been paid to the chemosensory studies in Limulus (Barber 1951, 1953, 1956) and spiders (Hodgson 1958a, 1958b). Limulus apparently has contact chemoreceptors on the mandibles and chelae and distinct chemoreceptors in a wart-like structure anterior to the mounth. There is considerable amount of controversy concerning the regional distribution of chemoreceptors in spiders. But the evidence indicates that they are widely distributed over the body especially in the mouth region. Thus while our knowledge about the sensory apparatus is poor in arthropods in general, it is more so with scorpion in particular. This can be justified from the statement by Hanson (1917) that in scorpion no other sensory hairs are known than the trichobothria. Later Hilton (1931) mentioned about the sensory hairs on the appendages of scorpion. The other earlier reports so far known on the sensory hairs were from Scheuring (1912) and Gossel (1935). Hodgson (1958a, 1958b) could not find any chemoreceptor hairs

in the few spiders he studied. The account by Rao (1964) showed that the scorpions have well developed chemosensory hairs both on the peipalps and the pectines. A survey of the literature thus revealed a complete lack of information on chemoreception in the large group of arachnids. Therefore the present attempt to study the chemoreception in scorpion using modern electrophysiological techniques assumes significance. As a consequence of the development of a hard sclerotized cuticle in scorpion the sensitivity to the external stimulus is confined to certain areas only. In these areas the response to the stimulus is made possible by the development of a multitude of sensilla of different categories. The histo-anatomical studies of the sensory structures in scorpion by Venkateswara Rao (1963) form a preamble for the present electrophysiological studies.

MATERIAL AND METHODS

Experimental animals

The experimental animal was the scorpion Heterometrus fulvipes, abundantly found in and around Tirupati. These animals were collected and kept in the laboratory in opaque troughs containing sand and stones to enable them to burrow during the day time. The animals were provided with water to drink and cockroaches to feed. In each batch of animals the mortality ranged between 3-5% over a period of 20 days to one month and it was more in the summer season. With careful attention the animals survived upto 2 months in the laboratory.

Pedipalps: Among the several appendages in the scorpions, only the pedipalps become powerfully developed. The distal segment of the pedipalp constitute the chela and is also known as the hand. These unique appendages are located on the second post-oral segment in the scorpion. They are prehensile and are intimately associated with the feeding apparatus of the animal. In the burrowing mode of life of scorpion the pedipalps are useful in digging. The pedipalps furnished with several sensory structures become all important to the scorpions and the behaviour of the animals ultimately depends on their efficiency.

Venkateswararao (1963) classified the sensory hairs present on the appendages of the scorpion H. fulvipes, into three distinct types a, b, and c basing on their structural

Legends for figures

Figs. 1 and 2 — Dorsal and ventral view of the pedipalp of scorpion Heterometrus fulvipes, respectively,

Cx - Coxa; Tr - Trochanter; Fm - Femur;

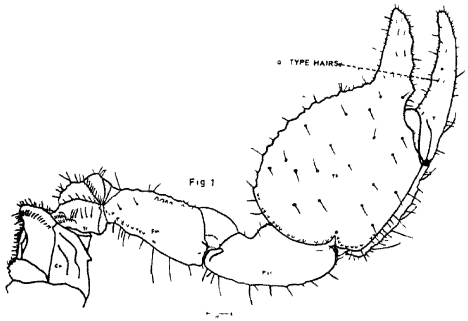
Pat - Patella; Tb - Tibia; T-Tarsus

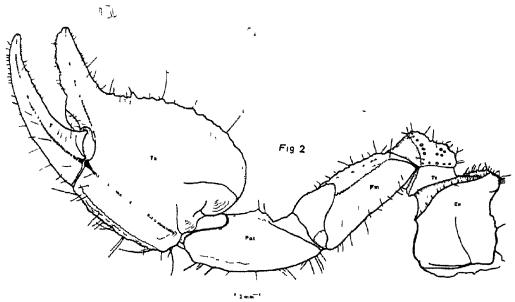
a - type 'a' hairs; b - type 'b' hairs

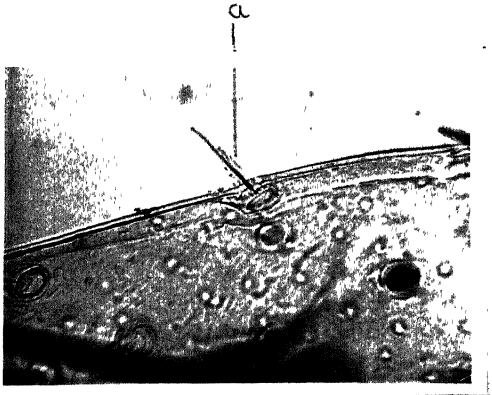
Note the denser distribution of 'a' hairs dorsally on the pedipalp.

Pm. 1. — Photomicrograph to show the external appearance of 'a' hairs (a) on pedipalp.

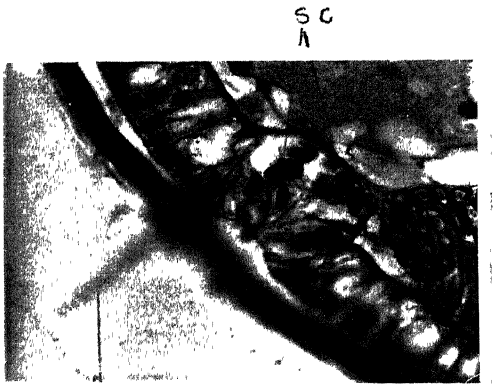
Pm. 2. — Photomicrograph of 'a' hair (a) and the sensory cells (S.C) in section.







Pm 1



Pm 2

variations. The 'a' type hairs (Figs. 1 and 2) are slender, short, thin walled and few in number interspersed with 'b' type hairs. The 'a' hairs are movably articulated with a small cuticular dome (Pm.I) and are supposed to respond to the chemical stimuli mostly on contact. The 'b' type of hairs (Figs. 1, 2 and Pm.3) are long and tapering. They occur in large number and are supposed to be mechanical in function. The type 'a' and 'b' hairs alone are present on the pedipalps and none of the 'c' type. The 'a' type hairs are mostly found on the dorsal surface (Fig. 1) and much less on the ventral surface (Fig. 2) of the hand and finger. They are rarely seen on the proximal segments.

Methods

The sensory responses of the 'a' type hairs were studied with different salts, sugars, and amino acids at varying concentrations. The pedipalp of an anaesthetized scorpion was amputated at the base and the cut end was immediately inserted in a silver cup containing fresh scorpion ringer solution. The silver cup was specially designed for this purpose and consists of a central pointed pin which acts as an indifferent electrode. The active electrode was designed to register the potential differences between the sensory surface at the tip of a single chemosensory hair and the cut end which is in direct contact with the indifferent electrode.

The same electrode will also serve as a vehicle for the chemical stimulus. The electrode is a piece of glass tube of 30 mm length. At one end its diameter (outer) is 3 mm while the other end was drawn out to a diameter of about 0.3 to 0.4 mm convenient enough to fit over the tip of a chemosensory hair. The glass capillary which serves as a stimulating and recording electrode was positioned over the tip of the hair with the help of a binocular microscope. The assembled electrode was mounted on a micromanipulator in such a fashion that it permitted a rapid and easy interchange of electrodes. The tip of the pedipalpal chemosensory hair (type 'a') was inserted into the recording electrode by operating the manipulator. The electrode was filled with fresh chemical solution under test. A thick Ag-AgCl wire, inserted at the untapered end of the capillary electrode, was connected with a high input impedance, cathode follower preamplifier followed by main amplifier (Tektronix type 122 with suitable cathode probe or Grass P-5 with cathode follower) and Oscilloscope (Philips GM 3156).

For recording the chemosensory impulses from the 'a' type hairs, the Hodgson and Roeder (1956) capillary electrode method was followed. In order to confirm the chemosensory role of 'a' hairs initial tests were carried out in 20 animals of different sizes and sex. Several 'a' hairs were tested in each preparation and all the records have shown evidence of spike potentials. Most of the preparations gave normal

and reproduciable responses for more than 60 seconds. Response was observed in many preparations for about 3 to 4 hours. Stimulation and recordings were done simultaneously. The responses were recorded for about 40 to 50 seconds. In the course of the experiments seperate glass capillary electrodes were used for the different chemicals. Fresh test solutions were prepared for each experiment.

Hodgson and Roeder (1956) showed that the frequency of impulses from insect chemoreceptors vary markedly with temperature changes. Frings and Cox (1954) have shown that temperature does influence the thresholds of behavioural responses of flies to stimulation of tarsal chemoreceptors. To minimise the influence of temperature variations on the receptor activity the whole experimental set up was arranged in an air conditioned chamber at a temperature of 22 $\pm$ 2° C. To avoid the external interferences the whole set up was arranged in a wiremesh cage.

The preliminary survey showed that the recovery period of a stimulated receptor varied with the nature, the concentration of the stimulus as well as the duration of the stimulus applied. However, the stimulated receptor recovered within a maximum period of 2 minutes. Therefore, three minutes recovery period was allowed for disadaptation of the receptor between the successive tests with a distilled water wash.

In the present studies only such salts, sugars and amino acids were used to which some of the animals were known

to give clear cut behavioural responses, because these compounds are encountered in the feeding, reproductive and orientation activities of the animals. The electrical activity of the receptor, displayed on the cathode ray oscilloscope screen (Phillips GM 3156) was photographically recorded on 35 mm film with oscilloscope camera (Philips voigtlander) and was simultaneously audiomonitored. The spike counts were made from approximately indentical records by visual inspection.

Stimulating but nonconducting chemicals like sugars, amino acids were dissolved in 0.1 M sodium chloride solution. It was not possible to use sodium chloride of a lower concentration because in the present investigation 0.1 M was known to be its threshold value. To ensure that the normal activity was maintained throughout the study, periodical tests were conducted with 0.1 M sodium chloride soulution.

Earlier studies on the threshold revealed differences in responses to a stimulus in a given species. There were variations in the general level of receptor activity in different preparations and also between the different hairs in the same preparation. In each concentration the responses were recorded in three seperate preparations. To minimise the above variations as far as possible the same hair was used both as control and for testing the responses at different concentrations of a compound. Attempts were made to record the responses of a receptor indifferent stimuli in a concentration range of

0.01 to 1.0 M at each stimulus. In each chemical the responses were recorded in a stimulus range of 1 to 20 volts. Each record was counted thrice by visual inspection and the averages were taken. The final averages of the spike counts from the reproduciable records of the different preparations were tabulated for intervals of ten seconds. The 'S' and 'L' spikes were designated depending on their heights. The spikes of about 50 μV were designated as 'S' spikes and those of about 50 μV or 100 μV as 'L' spikes. Other details not mentioned here will be reported in the results.

The sketches of pedipalps, pectines and legs were made with the aid of a camera lucida from the dissected preparations. Strong effort had been made to bring out as many structural details as possible. Several specimens were studied in order to avoid any pit falls due to individual variations. The type 'a' and 'b' hairs, pectines etc., were photographed from actual preparations and were inserted in the corresponding chapters.

RESULTS

Attempts were made to study the responses of 'a' type hairs on the padipalps with chlorides of sodium, potassium, magnesium, calcium, rubedium, lithium and caesium at concentrations 0.01 M, 0.025 M, 0.05 M, 0.1 M, 0.25 M, 0.5 M and 1.0 M. There was no response from the 'a' hairs with chlorides of magnesium, rubedium, lithium and caecium in the entire concentration range tested. The receptors responded in the chlorides of sodium, calcium and potassium but in each at different concentration ranges. When the receptor failed to respond at lower concentrations, attempts were made to study their responses at higher concentrations. In salts where the receptor responded over a wide range of concentrations the stimuli were applied in the ascending order of concentrations. The responses were recorded from a single hair at the different concentrations to obviate the response variations from hair to hair. The responses were mostly of single units with spike heights of about 50 μV. Each recording was counted thrice and the averages were noted. The data tabulated were the final averages of three preparations for intervals of ten seconds each. Individual variations between preparations in spike frequency were however present. The data were not treated statistically because the samples were too few and therefore the result would not be meaningful.

Responses of 'a' hairs with sodium chloride:

Although attempts were made to record the responses

with sodium chloride over a wide concentration range as mentioned above, the 'a' hairs responded at concentrations 0.1, 0.25, 0.5 and 1.0 M only. The receptor failed to respond at concentrations below 0.1 M indicating that it might be the threshold value for sodium chloride. Under similar experimental conditions the 'a' hairs on different preparations exhibited variations in the responses in each concentration of sodium chloride and they were reported with the graphs. The spike count at each interval was plotted against time intervals (Fig. 1).

The receptors exhibited progressively increasing responses with the concentration of the stimulating medium in a range of 0.1 to 1.0 M (Fig. 1). The increase in the responses was not proportional to the concentration of the stimulating medium. But when the logarithmic values of the spike frequencies in the different concentrations were compared the responses appear to increase approximately proportional to the concentrations. The initial lower responses with sodium chloride increased in the successive intervals while in chlorides of potassium and calcium it was the other way.

The receptors exhibited peak responses during different intervals which varied with the concentration of the stimu-

lating medium (Fig. 1)

n of different

Legends for plate 1.

Figs. 1 to 10 — Impulses of 'a' hairs of the caudal lobe of the crayfish Potamobius fluviles, with inorganic salts, sugars, mixtures and amino acids. Number of impulses for intervals of ten seconds each were plotted against time in seconds on semi-log graph paper. The vertical lines at each interval represent the standard deviation in the spike count between the different preparations.

Fig. 1 — 'L' fibre responses of 'a' hairs with sodium chloride at various concentrations in the four intervals.

Fig. 2 — 'L' fibre responses of 'a' hairs with chlorides of calcium and potassium at concentrations as shown.

Fig. 3 — 'L' and 'S' fibre responses with different sugars of 0.25 M mixed with 0.1 M sodium chloride.

Figs. 4, 5 and 5a. — 'L' and 'S' fibre responses, represented in lines of various shades with mixtures of sucrose and sodium chloride of different concentrations as shown below.

Fig.	Concentration of		Responses from	
	Sodium chloride	Sucrose	'L' fibre	'S' fibre
4.	0.1 M	0.1 M	Thick dashed and dotted line.	Thin dashed and dotted line.
	0.1 M	0.5 M	Thick dashed line.	Thin dashed line
	0.1 M	1.0 M	Thick continuous line.	Thin continuous line.
5.	0.5 M	0.1 M	Thick dashed and dotted line.	Thin dashed and dotted line.
	0.5 M	0.5 M	Thick dashed line.	Thin dashed line
	0.5 M	1.0 M	Thick continuous line.	Thin continuous line.
5 a.	1.0 M	0.1 M	Thick dashed and dotted line.	Thin dashed and dotted line.
	1.0 M	0.5 M	Thick dashed line.	Thin dashed line.
	1.0 M	1.0 M	Thick continuous line.	Thin continuous line.

Figs. 6 to 10 — 'S' and 'L' fibre responses in amino acids of 0.25 M mixed with 0.1 M sodium chloride. The dotted lines represent the 'L' fibre responses with sodium chloride of 0.1 M which was the control in all the tests.

PLATE - I

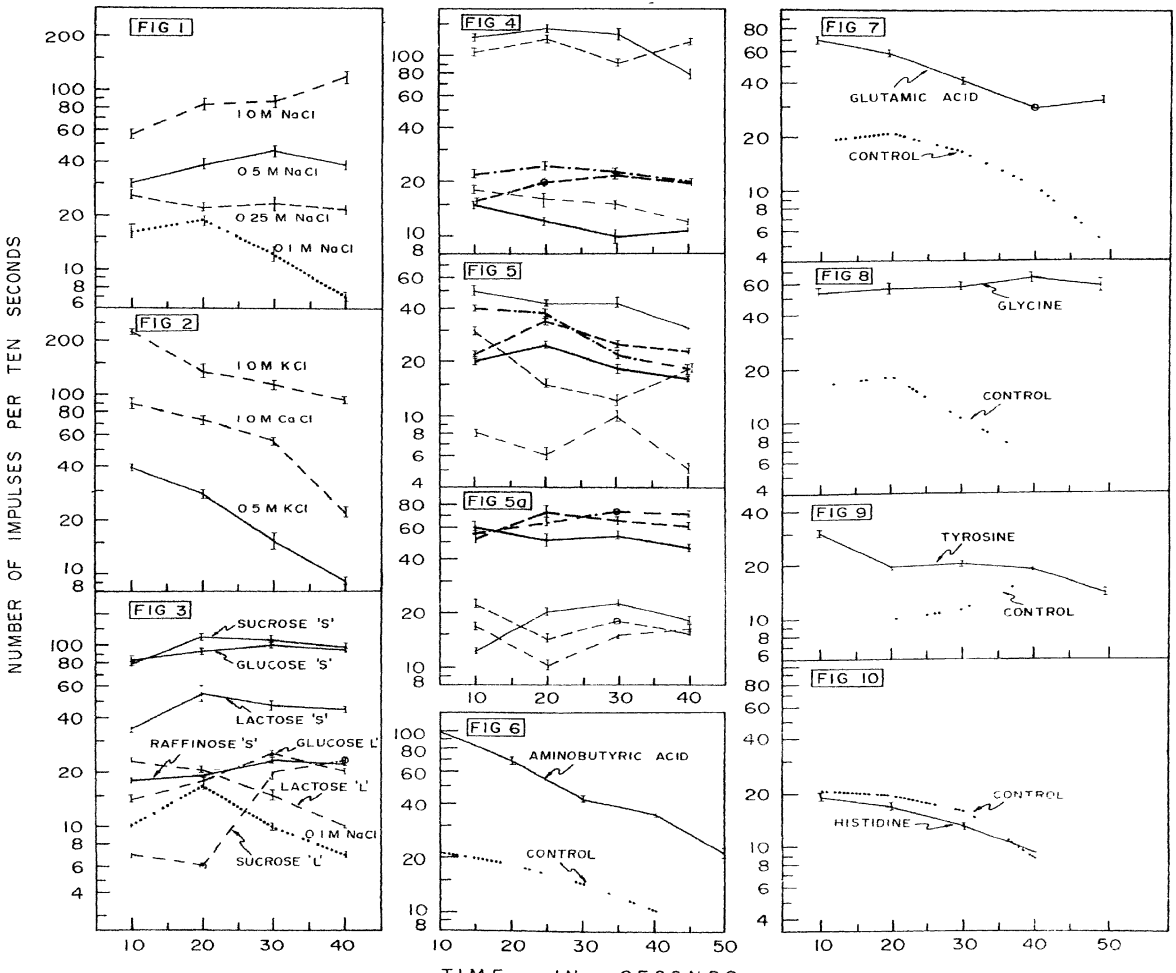


FIG 1
1 0 M NaCl
0 5 M NaCl
0 25 M NaCl
0 1 M NaCl
FIG 2
1 0 M KCl
1 0 M CaCl
0 5 M KCl
FIG 3
SUCROSE 'S'
GLUCOSE 'S'
LACTOSE 's'
RAFFINOSE 'S'
GLUCOSE 'L'
LACTOSE 'L'
0 1 M NaCl
SUCROSE 'L'
FIG 4
FIG 5
FIG 5a
FIG 6
AMINOBUTYRIC ACID
CONTROL
FIG 7
GLUTAMIC ACID
CONTROL
FIG 8
GLYCINE
CONTROL
FIG 9
TYROSINE
CONTROL
FIG 10
CONTROL
HISTIDINE
NUMBER OF IMPULSES PER TEN SECONDS
TIME IN SECONDS

concentrations the 'a' type hairs responded only at one concentration i.e., 1.0 M. The responses were studied in three preparations and variations in the responses were observed between receptors of the different preparations. The receptor exhibited a higher initial response followed by a gradual decline in the subsequent intervals unlike in sodium chloride (Fig. 2).

Responses of 'a' hairs with potassium chloride:

In potassium chloride the receptor was not responding at concentrations below 0.5 M and above 1.0 M. As in sodium chloride the receptor exhibited increasing responses with the increase in the concentration of stimulus medium. The responses in 1.0 M were too high in comparison with 0.5 M (Fig. 2). The initial maximal response decreased gradually during the successive intervals. In this respect the responses differ with sodium chloride but agree with calcium chloride.

The receptors on the three preparations exhibited variations in spike frequency and they were reported along with the graphs (Fig. 2).

Responses of 'a' hairs with carbohydrates:

Attempts were made to study the responses of 'a' hairs with sugars at various concentrations. The sugars being non-electrolytes, the test solutions were prepared by mixing them in an electrolyte of 0.1 M sodium chloride at its threshold concentration. Although attempts were made to record

the responses at various sugar concentrations, 0.25 M appeared to be more suitable for comparative study of both 'S' and 'L' fibre activity. The 'S' and 'L' spikes were designated as per the explanation given in the earlier chapter. The recordings were repeated on three preparations. In each preparation the responses with different sugars were recorded from the same receptor to obviate the individual response variations between the receptors. Each record was counted thrice and the final averages of the three preparations were noted. The average number of spike counts from the reproducible records were tabulated for intervals of ten seconds.

Among the sugars D-galactose, inositol and mannose were found non-stimulatory while the 'a' hairs responded with sucrose, glucose, lactose and raffinose. From the recordings spikes of two distinct types were observed, obviously one from 'S' fibre and the other from 'L' fibre. The 'S' fibre responds for the stimulus offered by sugars. In most of the sugars the initial lower response increased gradually with time. Maximal 'S' fibre activity was recorded with monosaccharides and the minimal with trisaccharides (Fig. 3).

With all the sugars the 'L' fibre activity was low in comparison with the 'S' fibre activity. The 'L' fibre activity was maximal with sucrose and minimal with lactose while with raffinose there was a total inhibition.

Responses of 'a' hairs with mixtures:

The responses of 'a' hairs were studied with mixtures of sodium chloride and sucrose changing the individual concentrations of each. Mixtures of the following concentrations were prepared for the study.

a) To the sodium cloride solution of 0.1 M were added separately sucrose of 0.1 M, 0.5 M and 1.0 M concentrations;

b) to the sodium chloride solution of 0.5 M were added seperately sucrose of 0.1 M, 0.5 M and 1.0 M concentrations and

c) to the sodium chloride solution of 1.0 M were added seperately sucrose of 0.1 M and 0.5 M and 1.0 M concentrations.

The testing of the responses was in the ascending order of the concentrations in the mixtures. The records show two spike units 'S' and 'L'. The 'S' and 'L' spikes were designated depending on their heights as reported earlier. In each preparation responses were recorded on the same hair and the readings were taken from three preparations. Each record was counted thrice and the averages were taken. The final averages of the spike frequency from the identical records were tabulated for intervals of ten seconds.

Responses of varying degrees were recorded from 'a' hairs depending upon the individual concentration of the salt and sugar in each mixture. With mixtures of 0.1 M

Legends for the films

Films to show the responses of the 'L' and 'S' fibres from the 'a' hairs of scorpion *L. fulvipes*, recorded at 10 volts with the following chemical compounds.

A. 'L' fibre responses with 0.25 M Sodium chloride. (spike height of about 50 μV).

B. 'L' fibre responses with 1.0 M sodium chloride (spike height of about 50 μV).

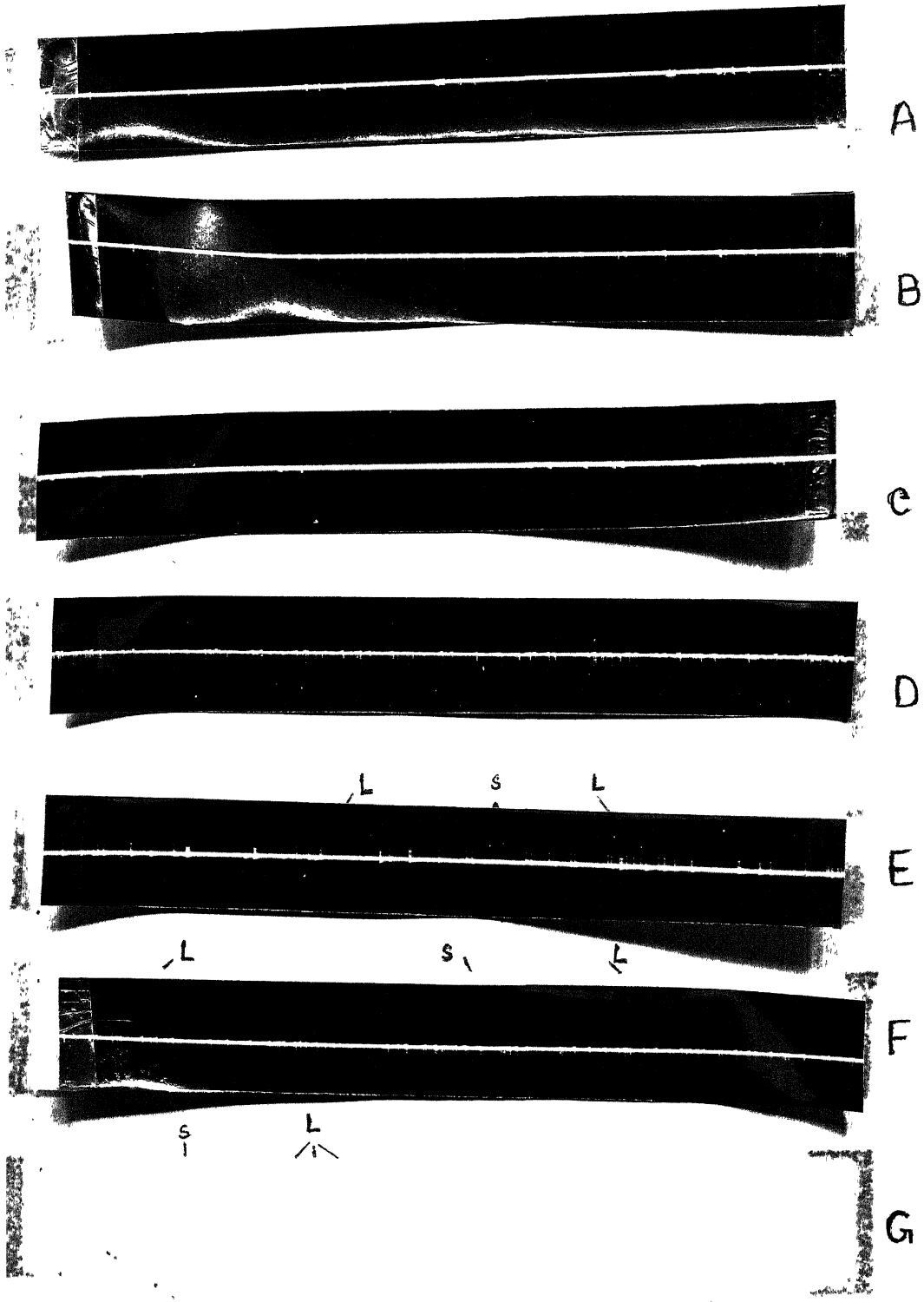
C. 'L' fibre responses with 1.0 M Calcium chloride (spike height of about 50 μV).

D. 'L' fibre responses with 0.5 M potassium chloride (spike height of about 50 μV).

E. 'L' and 'S' fibre responses with 0.25 M lactose mixed with 0.1 M sodium chloride ('L' spike height of about 100 μV and 'S' spike of about 50 μV. L and S on the film indicate the respective spikes).

F. 'L' and 'S' fibre responses of 'a' hairs with mixtures of 0.5 M sodium chloride and 1.0 M sucrose ('L' spike of about 100 μV and 'S' spike of about 50 μV. L and S on the film indicate the respective spikes).

G. 'L' and 'S' fibre responses with glutamic acid of 0.25 M mixed with 0.1 M sodium chloride ('L' spike of about 100 μV and 'S' spike of about 50 μV height. L and S on the film indicate the respective spikes).


A
B
C
D
L
S
L
E
L
S
L
F
S
L
G

sodium chloride + 0.5 M sucrose and 0.1 M sodium chloride + 1.0 M sucrose higher 'S' fibre responses were recorded while with mixtures of equal concentrations of salts (0.1 M) and sugar (0.1 M) higher 'L' fibre activity was recorded (Fig. 4). When tested with mixtures of 0.5 M sodium chloride and 1.0 M sucrose there was a higher 'S' fibre activity. With the other combinations (0.5 M salt + 0.5 M sugar and 0.5 M salt + 0.1 M sugar) the 'L' fibre activity was more than the 'S' fibre (Fig. 5) activity.

When examined with 0.1 M, 0.5 M and 1.0 M sucrose mixed seperately with 1.0 M sodium chloride higher 'L' fibre activity was recorded in all the combinations. The 'S' fibre activity was much lower (Fig. 5a).

Thus in a given mixture higher 'L' fibre responses were recorded when it contained either equal or higher salt concentrations than sugars while higher 'S' fibre activity was recorded only when the sugar concentrations were much higher in a given mixture.

Responses of 'a' hairs with Amino-acids:

The responses of the sensory hairs (type 'a') were studied with amino-acids like glycine, serine, arginine, aspartic-acid, tyrosine, histidine, glutamic-acid, and amino-butyric-acid at 0.25 M concentration. The non-conducting amino-acids were dissolved in an electrolyte of sodium chloride at 0.1 M concentration, its threshold value. The recordings were taken from four preparations. In each preparation all

the tests were carried out on the same hair. Both the 'S' and 'L' fibres responded with amino acids. The 'S' spike units (of about 50μV height) were numerically far more than the 'L' spike units (of about 100μV). Each reproduciable record was counted thrice and average number of spike counts were tabulated for intervals of ten seconds.

Among the acids tested there was a total inhibition of response with serine, arginine and aspartic-acid. No response was obtained in these acids even at higher concentrations. In histidine the stimulus effect was too small to be of any significance (Fig. 10). Very low response was obtained in tyrosine (Fig. 9) while fairly good responses were recorded in aminobutyric-acid, glutamic-acid and glycine (Figs. 6, 7, and 8). The initial high response in tyrosine, aminobutyric-acid and glutamic-acid was decreased in the successive intervals indicating a tendency for adaptation. In glycine the peak response was observed only in the fourth interval.

DISCUSSION

It is known that the number of compounds that the insects could detect was very great and that different receptor cells in a contact chemoreceptor hair respond specifically to different chemicals. The responses of the 'a' type hairs on the pedipalps were studied with chlorides of sodium, potassium, calcium, magnesium, rubedium, lithium and caesium at different concentrations. Among them the 'a' hairs responded only in the chlorides of sodium, potassium and calcium. In sodium chloride the response was noticed in a certain concentration range and it varied with the concentration (Fig. 1). Concentrations of calcium chloride of less than 1.0 M and potassium chloride of less than 0.5 M apparently did not evoke any response. But Hodgson and Roeder (1956) reported that the chemoreceptor hairs of blowfly responded with potassium chloride even at much lower concentration of 0.2 M. The salt stimulated only the 'L' fibre and the nature of the response appeared to be much the same as in sodium chloride.

Evans and Mellon (1962) studied the responses of the salt receptor cells of the taste sensilla of a blowfly in various salts. They observed that only the salts of potassium elicited a response in the pattern of sodium chloride. Further they observed responses also with chlorides of rubedium, lithium and caesium, while in the present studies no such responses were observed with several of these salts.

When the spike frequencies of the receptor in the various salts were compared, the highest initial response was noticed with potassium chloride followed by chlorides of calcium and sodium. Thus the magnitude of the responses exhibited by the sensory hairs seem to vary with the nature of the salt tested. From the sequence of spike frequency a possible correlation appears to exist between the stimulative efficiency of the salt and its ionic mobility. From his studies on Cercopea moth larva, and Periplanata americana, Frings (1945, 1946) showed a similar relation for several series of salts with a common anion like bromide, chloride and iodide. Similar findings were reported subsequently by Frings and O'Neal (1946), Detheir (1947C, 1955a), Frings (1948) and Hodgson (1951). While studying the responses of the taste receptors of the mosquito, Salama (1966) also concluded that the stimulating efficiency of cations with a common anion combination could be correlated to their ionic mobilities. The present findings were in good harmony with those of Salama. Explaining the significance of the ionic mobility and the stimulating efficiency Osterhout, Kamerling and Stanley (1934) stated that the penetration of the salts through the membrane of the receptor cells is in accordance to the order of the ionic mobility. Therefore, the ionic mobility must determine the stimulating efficiency of a salt under examination. The sequence of responses obtained in the present investigation were in agreement with the abo

explanation.

The spike frequency increased progressively with increasing concentrations of sodium chloride ranging from 0.1 M to 1.0 M (Fig. 1). Thus a correlation appears to exist between the chemical stimulus concentration and the spike frequency in the excited fibres. This observation was identical with the findings reported from the studies of the sense of taste in mammals by Pfaffmann (1941) and Beidler (1953). They have shown that in both insects and mammals there was a rapid increase in the frequency of firing as the concentration of the stimulant was raised above threshold. Later Hodgson and Roeder (1956) reported a similar increase in the response of the chemoreceptor hairs of blowfly when the strength of the sodium chloride solution was raised above threshold. Beidler (1954) made an attempt to explain the possible reasons for such a correlation between the magnitude of response and the concentration of the stimulating media. In the openion of Beidler (1954) the magnitude of the response in mammalian receptors was directly related to the number of ions or molecules present in a test solution which would react with the receptors and produce the differential responses.

In 1.0 M and 0.5 M potassium chloride the sensory hairs exhibited a higher initial response. But in subsequent intervals (Fig. 2) there was a rapid decrease in the response. This trend appears to be in agreement with the findings of Pfaffmann (1959). In the openion of Pfaffmann when a single

receptor was stimulated successively it leads to a decrease of its sensitivity in course of time. Therefore, the higher initial frequency range of impulses decreases gradually as reported in the present investigation. He showed further that the decrease in sensitivity was proportional to the intensity and duration of adapting stimulus. Thus in the present study the initial quicker drop and the successive slower drop in the frequency of impulses hints at a possible initial quicker rate and then a slower rate of adaptation to the stimulus provided by potassium chloride. The present pattern of response noticed with potassium chloride was in agreement with the findings of Hodgson and Roeder (1956) with sodium chloride although in the present studies there was no tendency for adaptation in sodium chloride. They showed that 0.5 M sodium chloride stimulation may result in considerable adaptation during the first one second interval followed by a less rapid decline in activity for the next few seconds but with a subsequent steadiness or a very slow decline in the discharge frequency.

While with all the sugars the 'S' fibre exhibited higher activity, the 'L' fibre exhibited either very low activity or was totally inhibited as with raffinose. The gradation in the spike frequency followed a definite pattern. A correlation appears between this pattern of activity and the structural configuration of the sugars tested. Von Frisch (1935) and Wykes (1952) concluded that some biological

specificity might be involved in stimulation of the honey-bee by sugars. Dethier (1955a) showed the significance of the structural configuration of a sugar in the stimulation of the blowfly. Salama (1966) observed that compounds like mannose, turanose and sucrose with α-linkage were superior stimulating agents. Lactose, melibiose and cellobiose which lack the α-linkage were either weak or non-stimulating. D-arabinose and D-xylose were more stimulating than the respective α-forms. Therefore the structure of the molecule appears to be a deciding factor in stimulating the 'S' fibre response.

When mixed stimuli were applied to the chemosensory hairs responses of varying degrees were recorded depending upon the concentrations of individual salt and sugar in a given mixture. If, in a mixture the sugar concentration was more than the salt a higher 'S' fibre activity was observed (Figs. 4 and 5). On the other hand if, in a mixture the salt was present either in equal or in higher concentrations a higher 'L' fibre activity was noticed (Figs. 4, 5, and 5a). Thus the higher 'S' fibre activity and the inhibition of 'L' fibre activity in higher sugar concentrations and the higher 'L' fibre activity and the inhibition of 'S' fibre activity in equal or higher salt concentrations in mixtures suggest an inverse relationship between the 'S' and 'L' fibre activity. The responses exhibited by the 'S' and 'L' fibres in the present studies were in agreement with Hodgson (1956a, 1957),

Morita, Doira, Takeda, Kuwabara (1957), Wolbarsht (1958), Morita and Takeda (1959), Morita (1959), Stürckow (1959) and Takeda (1961).

From the studies on the maxillary chemoreceptors of silkworm Bombyx mori, Ishikawa (1963) showed that the high concentration of the sodium chloride in the low concentration of sugar solution generally depressed the frequency of the sugar receptor impulses. Further he demonstrated that with the increase in concentration of sodium chloride mixed in sucrose solution the frequency of 'S' impulses was gradually diminished and finally the impulses responding for sodium chloride occured. The findings of Ishikawa (1963) agree with the present studies to a large extent. From the studies on Vanessa, Takeda (1961) explained that the depression in the frequency of impulses from the sugar receptor in the presence of sodium chloride represents a direct inhibitory effect. In very low concentrations of sodium chloride (0.031 M - 0.062 M) the recordings by Hodgson and Roeder (1956) showed responses predominantly in the 'S' fibres with infrequent responses from 'L' fibres. However, higher concentrations of sodium chloride caused typical 'L' fibre responses in the same hairs.

Behavioural and electrophysiological studies by earlier workers have indicated the presence of chemoreceptors particularly sensitive to amino-acids. Sufficient information regarding the chemoreception in Arthropods had accumulated

(Luther 1930; Hodgson 1958b; Case, Gwilliam and Hanson 1960; Case and Gwilliam 1961; Barber 1961). But to the best of our knowledge no reference had been made so far about Arachnids. The food of the scorpion H.fulvipes, mostly consists of juices of insects and related species. Amino-acids occur naturally in insect tissues relatively in higher concentrations. Thus from the behavioural point of view the responses of the scorpions to the amino acids appear to be most important. Among the amino acids tested there was a total inhibition of response in serine, arginine and aspartic acid, while a partial inhibition was noticed in histidine (Fig. 10). In tyrosine (Fig. 9) there was only slight response while in aminobutyric acid, glutamic acid and glycine fairly good responses were recorded (Figs. 6, 7 and 8).

Since earlier studies on the Arachnid group were lacking these results could be compared with the findings on Crustacea which appear particularly suitable for the study of chemoreceptors sensitive to amino acids and amines. Hodgson (1958b), Case and Gwilliam (1961) noted receptors in crayfish and crabs sensitive to amino-acids especially to glutamic acid in related species. In an electrophysiological examination of the dactyl innervation of the European Carcinus, Laverack (1963) was unable to detect responses to amino acids. In the subsequent studies on the dactylopodites of Cancer productus Randall, and C.antennarius Stimpson with amino acids, Case (1964) has made interesting observations. He

demonstrated the existence of dactyloamino acid receptors in the above species by considering their chemical sensitivity in detail. He found that among the most effective compounds are DL - α - amino - N - butyric acid, aurine, L-glutamic acid and serine in descending order of activities. The present studies were in agreement with Case (1964) as far as a higher response was noticed in aminobutyric acid and glutamic acid. While Case (1964) observed lowest response in serine a total inhibition was noticed here.

In the present investigation with tyrosine, aminobutyric acid and glutamic acid the tendency was towards a quick adaptation from an initial higher response (Figs. 6, 7 and 9). Case (1964) also reported a similar trend towards a rapid adaptation.

From these studies it is evident that type (a' hairs on the pedipalps are primarily concerned with chemoreception.

SUMMARY

1) In scorpion Heterometrus fulvipes, the pedipalps are the powerfully developed appendages and are furnished with several sensilla like 'a' hairs. The 'a' hairs distributed mostly on the dorsal surface of the hand and finger are supposed to respond to chemical stimuli on contact.

2) The chemoresponses of the 'a' hairs were studied with several inorganic salts (at varying concentrations), sugars, mixtures of sugars and salts and a amino-acids.

3) Among the inorganic salts the number of compounds that the scorpions could detect by means of the 'a' hairs are very few (sodium chloride, calcium chloride and potassium chloride only) in comparison with the insects. The concentration range within which the 'a' hairs are stimulated is limited (0.1 to 1.0 M only) from the insect standards. The responses varied with concentration and the ionic mobility of the salts.

4) The scorpions could detect very few sugars. The 'S' fibre activity in the different sugars suggests a correlation between the stimulative efficiency and the structural configuration of the sugars. The sensitivity of the receptors was in the descending order from sucrose, glucose, lactose and raffinose.

5) When mixed stimuli (sucrose + sodium chloride) were applied, the varying concentrations of the salt and

sugar appear to influence the pattern of 'L' and 'S' fibre activity. In the present studies an inverse relation was observed in the responses of the 'L' and 'S' fibres.

6) The 'a' hairs elicited responses in few amino-acids only. The responses varied between total inhibition to good response. The stimulating efficiency was in the descending order from aminobutyric acid, glutamic acid, glycine, tyrosine and histidine while there was a total inhibition in serine, arginine and aspartic acid.

7). Thus the 'a' hairs appear to be concerned primarily with contact chemoreception. From the standards of insects the scorpion H.fulvipus could be rated as a detector of the chemical compounds within many limitations.

CHAPTER II

SENSORY RESPONSES FROM THE PECTINES

INTRODUCTION

The role of the Pectines was a source of controversy ever since Dumeril (1806) considered them as external respiratory organs. In the mean while several other functions were assigned to the pectines until Gaubert (1889) discovered that the pectinal teeth have a rich innervation and that these appendages are undoubtedly sense organs. By virtue of their location near the genital aperture Pocock (1893) concluded that they are tactile organs associated with sexual function and with the descrimination of the nature of the terrain on which the animal walks. Warburton (1909) also shared the openion of Pocock and assumed that the pectines are tactile organs. Gaskell (1902) regarded pectines as auditary and balancing organs. The first detailed histological study of the pectines seem to have been made by Schroder (1903). He concluded that the pectines are chemotactile organs with dual role as receptors for taste and smell. According to Snodgrass (1935) the pectines are provided with different kinds of sensilla which can respond to the mechanical as well as chemical stimuli thus acting as mechano and chemoreceptors. Cloudsley-Thompson (1955) believed that the pectines are concerned in the perception of ground vibrations and are used more in warning of the danger than in the detection of prey. Alexander (1957) believed that the sensilla on the pectines are capable of sensing the texture of the substratum. Hoffmann (1964) concluded that the sensilla on the pectines are sensitive for the vibrations. Reddy (1965)

observed that the sensilla on the pectines serve both as hygroceptors and olfactory sense organs.

Thus a review of the literature revealed a lack of electrophysiological studies to assess the actual role of the sensilla on the pectines. Therefore, the present study is an attempt towards a general survey of the functions of the sensilla on the pectines using the modern electrophysiological techniques.

MATERIAL AND METHODS

The experimental animals selected for the study of the sensory responses from the pectines was the scorpion Heterometrus fulvipes, mentioned in the preceeding chapter. The details regarding the rearing of the animals in the laboratory and the other precautions observed are the same as reported in the previous chapter.

In scorpions the pectines are unique appendages situated on the second mesosoma. Each pectine is composed of three longitudinal series of pieces, the dorsal or the main piece, the fulcra and the pectinal teeth. The pectinal teeth are inserted on the fulcra. The pectines are furnished with a large number of sensilla (Figs. A & B). The sensilla fall under three categories: 1. the sensory bristles 2. Slit sense organs and 3. Peg sense organs. The sensory bristles fall under two types namely the type 'b' hairs and the white stiff hairs. The 'b' hairs are long and thick walled (Pm. 3). They are confined to the anterior border and ventral surface of the anterior row of the three plates forming the main shaft of the pectine (Fig. A and B). The white stiff hairs are much smaller in size than 'b' hairs and are located on the dorsal surface of the fulcral plates (Fig. A). On each plate 2 to 4 hairs are situated. The sensory pegs are similar to the sensilla basiconica of the insects (Pm. 4) and are situated in large numbers on the pectinal teeth dorsally. Type 'a' hairs are absent on the pectines.

Legends for figures.

Figs. A and B. Dorsal and ventral views of pectine of scorpion H.fulvipes, respectively. Note the densly distributed sensilla on the dorsal side (Fig. A) and their absence on the ventral side (Fig. B) of the pectine.

Pm. 3 Photomicrograph to show the external appearance of 'b' haris (b) on pectine.

Pm. 4 Photomicrograph to show the dorsal view of the pectinal teeth (P.T) along with the sensory pegs (S.P), the fulcral plates (F.P) and the 'b' hairs (b) on the main shaft.

Fig A

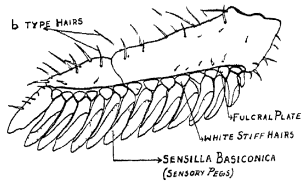
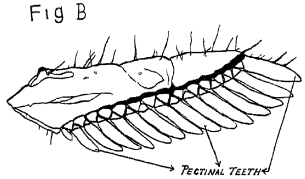
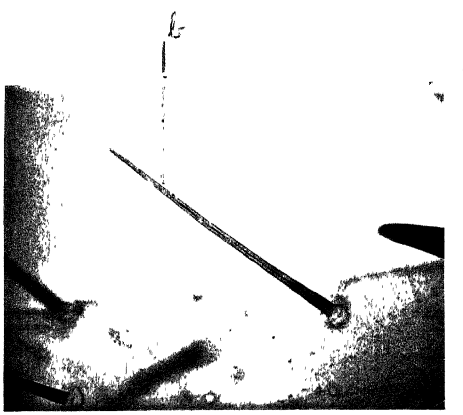
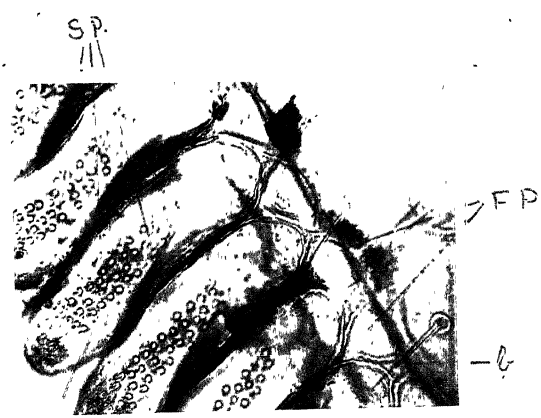


Fig B





Pm. 3.



Pm. 4.

RESPONSES FROM THE SENSORY PEGS

The responses of the sensory pegs on the pectinal teeth were studied with various salts, sugars, amino acids at different concentrations. The pectine of a lightly anaesthetized scorpion was amputated at the base and the cut end was inserted in a silver cup containing fresh scorpion ringer. The pointed pin in the centre of the silver cup acts as an indifferent electrode. The active electrode of a suitable tip diameter, the details of which were reported in the earlier chapter, was positioned with the help of a a binocular microscope over the tip of a sensory peg. The assembled electrode was mounted on a micro-manipulator. The electrode was filled with fresh test chemical solution, and a thick Ag-AgCl wire was inserted at the other end of the capillary. The electrode was connected with a high input impedance cathode follower pre-amplifier followed by main amplifier (Tektronix type 122 with a suitable cathode probe or Grass P-5 with cathode follower) and oscilloscope (Philips GM 3156). The sensory impulses were recorded from the sensory pegs using Hodgson and Roeder (1956) capillary electrode method. The same procedure and precautions mentioned in the early chapter were followed in the present studies in recording the spike frequency.

The experimental set up was arranged in a wire-mesh cage inside an air-conditioned chamber at a temperature of $22 \pm 2^{\circ}$ C. The preliminary tests were made on 15 separate

preparations and all the records have shown evidence of spike potentials. It was also observed that the responses varied with the concentration of a compound. The responses were recorded at a stimulus strength of 10 volts. Three minutes recovery period was allowed for disadaptation of the receptor between successive chemical tests with a distilled water wash. The other details not mentioned here will be reported in the results.

OTHER SENSORY RESPONSES FROM THE PECTINAL SENSILLA:

The scorpion was fixed to a wax block ventral side up and the pectinal nerve was exposed without damaging the pectine and was lifted onto the Ag-AgCl electrode. A drop of paraffin oil and vaseline mixture was applied to the exposed part of the nerve to prevent drying. The responses of the sensory pegs and the immediately surrounding sensory area on the pectine were recorded by exposing the pectinal teeth to swabs of xylene, benzene and toluene.

The mechanical responses of the pectinal sensilla were studied as reported below:

a) The sensory pegs were stimulated at frequencies of 15,60 and 120 CPS by a fine metal pin of tip diameter of 3 to 5 micra attached to the diaphragm of a small loud speaker which in turn was activated by an audio-oscillator. The responses from the sensory pegs were recorded from the pectinal nerve.

b) Further the responses of sensory pegs by stimulating them with horse tail bristles,

c) the responses of the 'b' hairs by stimulating with a needle,

d) the responses of the white stiff hairs on the fulcral plates by stimulating with horse tail bristle and

e) the responses of the sensilla on the pectines by blowing continuous and puffs of air, were also studied.

RESULTS

The responses of the sensory pegs of the pectinal teeth were recorded in a) inorganic salts b) sugars c) amino acids and d) 'cockroach smoke water'.

Attempts were made to record the responses with the chlorides of sodium, calcium, potassium, magnesium, rubedium, lithium and caesium at concentrations of 0.01 M, 0.025 M, 0.05 M, 0.1 M, 0.25 M, 0.5 M, and 1.0 M. The stimulus was applied in the ascending order from the lowest concentration. The recordings were made at a stimulus of 10 volts. In each preparation records were taken from the same sensory peg at different concentrations in order to obviate the response variations between the different sensilla. The responses were mostly of single units. Each recording was counted thrice and the averages taken. The final averages of the recordings of four preparations were calculated for intervals of ten seconds each. Individual response variations between preparations were however present, and they were reported along with the graphs.

Amongh the inorganic compounds tested the receptor responded only with the sodium chloride at concentrations of 0.1 M, 0.25 M, 0.5 M, and 1.0 M. The spike frequency for intervals of ten seconds each in the different concentrations of sodium chloride were plotted in the graph (Fig. 11). The spike frequency increased with the concentration of the sodium chloride. The sensory peg exhibited relatively high responses in 1.0 M than in the other concentrations. An initial high

response was noticed at all the concentrations of sodium chloride (Fig. 11). In sodium chloride while the sensory pegs exhibited higher initial responses the 'a' hairs exhibited higher responses only in the subsequent intervals. When the responses were studied by applying the stimulus successively the following trends were noticed. In concentrations of 0.5 M and below, there was a rapid drop in the spike frequency between the first and second intervals, followed by a slower rate of decrease. But in higher concentration (1.0 M) the rate of drop in the spike frequency was at a very slow rate between the first and second intervals followed by a rapid drop in the successive intervals (Fig. 11). The decline in the rate of the spike count in the successive intervals indicates a possible adaptation of the receptor to the stimulus.

Responses of sensory pegs with carbohydrates:

The responses of the sensory pegs were studied with different sugars like glucose, sucrose, lactose, raffinose, D-galactose, inositol and mannose at various concentrations. The test solutions were prepared by mixing the different sugars in an electrolyte like sodium chloride at 0.1 M concentration, its threshold value. From an earlier survey sugar concentration of 0.25 M was found to be more suitable for the production of spike frequency at a stimulus strength of 10 volts. The responses with the different sugars were recorded from the same receptor. The responses were studied on four separate

Legends for plate 2

Figs. 11 to 14. Responses from sensory pegs of scorpion *M. fulvipes* with inorganic salts, sugars, amino acids etc. In each figure the number of impulses per ten seconds interval (spike heights of about 50 μV) were plotted against time in seconds. The range of spike count variation between the different preparations in the four intervals at each concentration was given below.

Fig. 11. '$' fibre responses with sodium chloride at different concentrations. Range of spike count variation between preparations. At 1.0 M NaCl - ± 2 to 6; at 0.5 M NaCl - ± 2 to 4; at 0.25 M NaCl - ± 2 to 4 and at 0.1 M NaCl - ± 2 to 3.

Fig. 12. 'S' fibre responses with sugars of 0.25 M concentration mixed with an electrolyte of 0.1 M NaCl. Range of spike count variation between preparations.

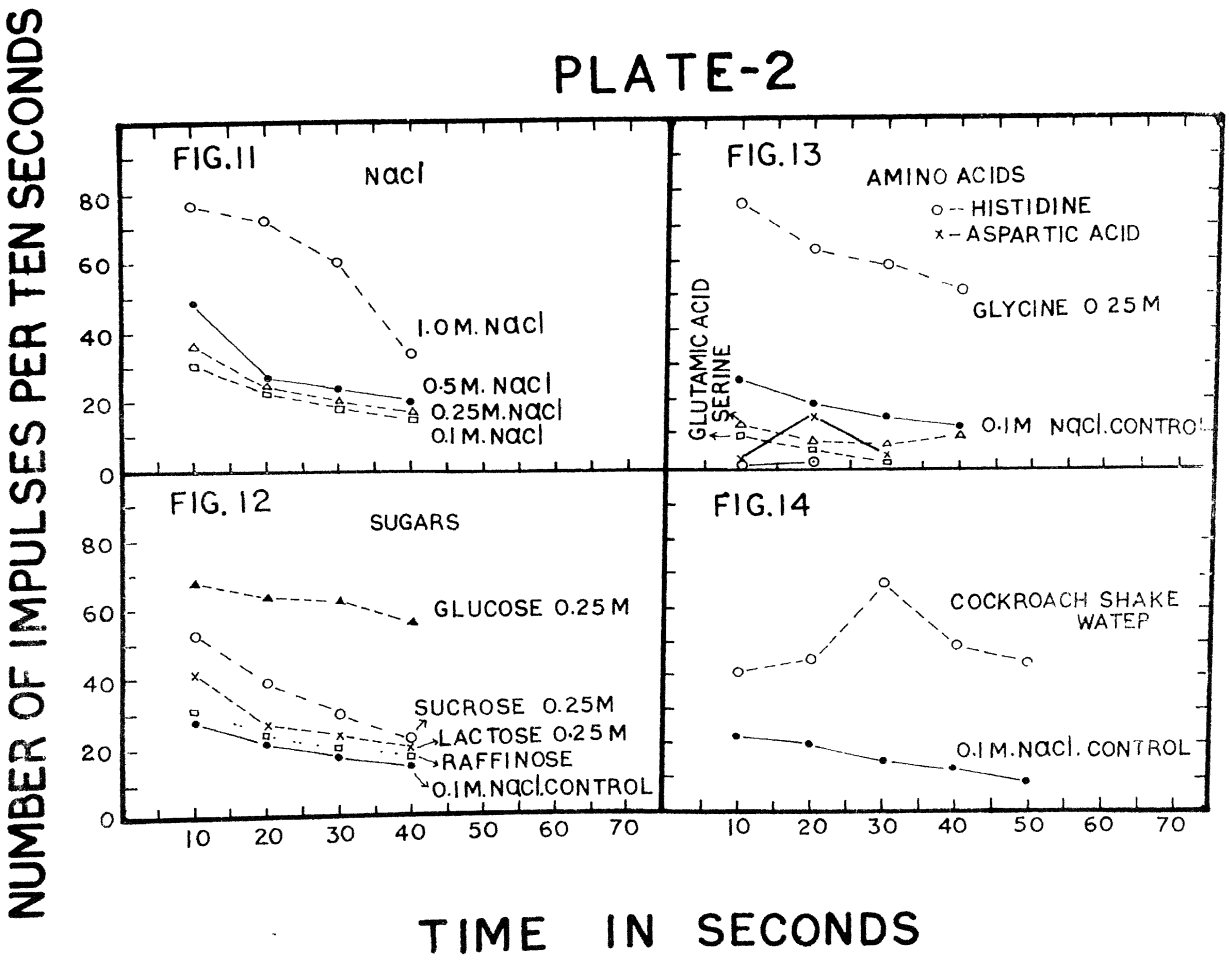
Glucose - ± 3 to 6; sucrose - ± 2 to 5
Lactose - ± 2 to 4; raffinose - ± 1 to 4

Fig. 13 'S' fibre responses with amino acids of 0.25 M + 0.1 M NaCl. Range of spike count variations between preparations.

Glycine - ± 4 to 6; serine - ± 1 to 3
glutamic acid - ± 1 to 2.

Fig. 14 Responses in 'Cockroach shake water.' Range of spike count variations between preparations ± 3 to 6.

PLATE-2


NUMBER OF IMPULSES PER TEN SECONDS
FIG.11
NaCl
1.0 M. NaCl
0.5 M. NaCl
0.25 M. NaCl
0.1 M. NaCl
FIG.13
AMINO ACIDS
o -- HISTIDINE
x -- ASPARTIC ACID
GLYCINE 0.25 M
GLUTAMIC ACID
SERINE
0.1 M NaCl. CONTROL
FIG. 12
SUGARS
GLUCOSE 0.25 M
SUCROSE 0.25 M
LACTOSE 0.25 M
RAFFINOSE
0.1 M. NaCl. CONTROL
FIG.14
COCKROACH SHAKE WATER
0.1 M. NaCl. CONTROL
0
20
40
60
80
10
20
30
40
50
60
70
TIME IN SECONDS

preparations. Each record was counted thrice and the averages calculated. The final averages of the spike count of the four preparations were tabulated at intervals of ten seconds. The variations in the responses between preparations were reported along with the graphs. The spike count at intervals of ten seconds in each sugar was plotted against time in seconds (Fig. 12).

Among the sugars D-galactose, inositol and mannose were found non-stimulatory. The sensory pegs responded with glucose, sucrose, lactose and raffinose. Responses were elicited from the 'S' fibres only while there was a total inhibition of 'L' fibre response. When tested with the same sugars the 'L' fibre responses in the 'a' hairs were not totally inhibited as noticed in the sensory pegs.

Among the sugars tested the maximal action potentials were elicited with glucose and mimimal with raffinose. With sucrose and lactose the responses were median (Fig. 12). It is interesting to note that the degree of responses exhibited by the sensilla with the various sugars follow a pattern which has some correlation with the structural configuration of the sugars under examination. The gradual decrease in the spike frequency elicited by the sensilla during the successive intervals in the present study indicates a tendency towards adaptation to the stimulus.

In sucrose and lactose a quick rate of adaptation was noticed when compared with glucose and raffinose.

Responses of sensory pegs with amino acids:

The responses of the pegs were studied with amino acids, glycine, serine, glutamic acid, aspartic acid, histidine, aminobutyric acid, arginine and tyrosine. From the preliminary survey 0.25 M appeared to be a convenient concentration for a comparative study of responses with the different amino acids. The amino acids being non-electrolytes, were mixed with sodium chloride at a concentration of 0.1 M, its threshold value. The responses in the different acids were recorded from the same sensilla at a stimulus of 10 volts. The responses were recorded from four separate preparations. Both the 'S' and 'L' fibres responded with amino acids. But the responses elicited by the 'S' fibres were higher than the 'L' fibres. The spike count at intervals of ten seconds were plotted against time (Fig. 13).

The sensilla evoked responses with glycine, serine, glutamic acid, aspartic acid and histidine. There was a total inhibition of responses with aminobutyric acid, arginine and tyrosine. The recoptor exhibited fairly good response with glycine only while with serine, glutamic acid, aspartic acid and histidine very low or partially inhibited responses were recorded. With glycine the receptor exhibited a tendency for adaptation. With other acids there was no clear cut trend towards adaptation.

"Cockroach Shake water": 10 ml of 0.1 M sodium chloride solution was shaken for five minutes keeping a live cockroach inside and the animal was removed from the solution later.

This is "Cockroach shake water". The response of the sensory pegs with the "Cockroach shake water" was tested. The initial response was low. The maximal response was elicited in about 30 seconds followed by a gradual decrease which indicates that the receptor was tending towards adapation to the stimulus.

Responces were also recorded from the pectinal nerve exposing the sensory pegs and the immediately surrounding area on the pectinal teeth to swabs of xylene, benzene, and toluene. Maximal responses were recorded with xylene and minimal with toluene. Similar responses could not be recorded when other appendages possessing contact chemoreceptors like 'a' hairs were exposed to the same vapours.

Mechanical responses from the pectinal sensilla:

A general survey was attempted to assess the role of the different sensilla like the sensory pegs, type 'a' hairs, white stiff haris by subjecting them to mechanical stimulus.

When the sensory pegs (Pm. 4) were touched with a horse tail bristle there were responses from the pegs in the form of smaller spikes. Later the pegs were stimulated with a fine metal pin of tip diameter of 2 to 3 micra. The pin was attached to a small loud speaker diaphragm and vibrated at frequencies of 15, 60 and 120 cycles per second (CPS). It was found that the pegs were exhibiting higher responses with increased frequencies of 15, 60 and 120 CPS. From the records at a frequency of 120 CPS more than one spike units were noticed.

~~Legends~~ for the film

Films to show the electrical responses of the different sensilla on the pectine of the scorpion, *P. fulvipes*, recorded from the pectinal nerve at 10 to 1 volts stimulating shock as follows.

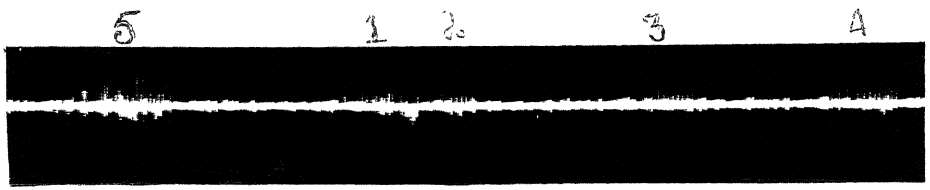
A. Responses from the 'D' hairs bending them with a fine needle. In the film Nos. 1, 2, 3 and 4 the spikes obtained when the hairs were bent gently and No. 5 when more pressure was applied to the hairs.

B. Responses from the white stiff hairs when touched with horse tail bristle. In the film Nos. 1, 2, 3 and 4 indicate the spikes when more pressure was applied on the hairs.

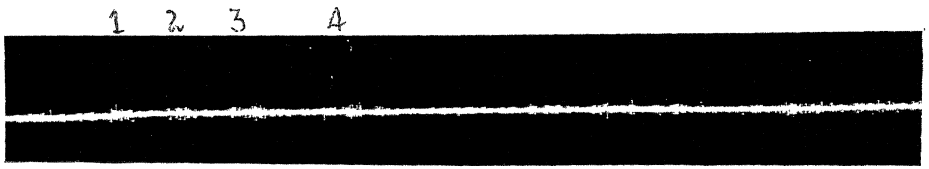
Responses recorded from the pectinal nerve when a stream of air was blown continuously. The responses for the blowing of air commenced from ~~the arrow mark.~~ no. 1

D. Responses recorded from the pectinal nerve when puffs of air was blown towards the pectinal surface. In the film Nos. 1, 2, 3 and 4 indicate spike units when air was blown in puffs.

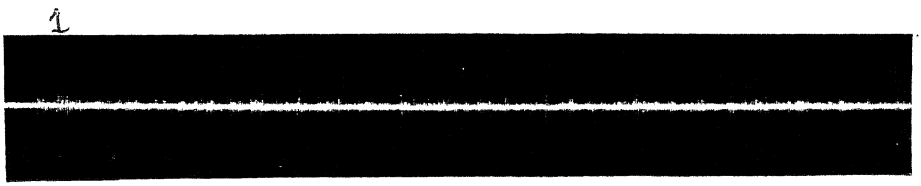
E. Responses of sensory pegs when stimulated at 120 CPS by means of a fine metal pin attached to the diaphragm of a speaker. Note the units of more than one type.



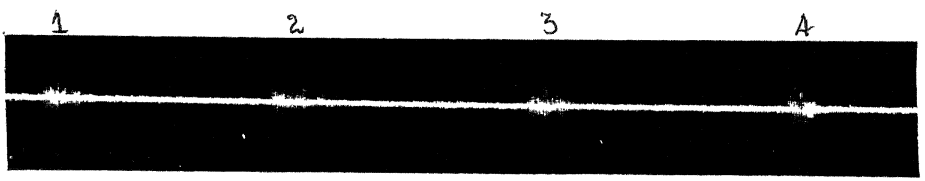
A



B



C



D

E

By stimulating the 'b' hair (Pl. 3) with a fine needle the responses were recorded from the pectinal nerve. From the records it appear that depending on the pressure applied by the needle on the 'b' hair the length of the spike units seem to vary. Increased pressures seem to produce larger spike units (Fig. a).

The white stiff hairs on the fulcral plates were stimulated with a horse tail bristle and the responses were recorded from the pectinal nerve. The records show that the white stiff hairs were responding to mechanical stimulus. Depending upon the pressure applied on the hairs the responses also changed resulting in the production of at least two spike units in the present studies (Fig. b).

By blowing air in puffs and continuously the responses of the sensilla of the pectinal surface were recorded. When the air was blown in puffs the responses were obtained in the form of bursts (Fig. C). On the other hand when a continuous air stream was blown towards the sensilla the responses were in the form of more or less idential spike units (Fig. d).

DISCUSSION

From the tests conducted on the 'a' hairs of the pedipalps it was inferred that the scorpions could detect fewer number of compounds in contrast to the insects. While it was so in the case of 'a' hairs the sensory pegs could distinguish still lesser number of compounds. When the responses of the pegs were tested with the chlorides of sodium, potassium, calcium, magnesium, rubedium, lithium and caesium the pegs were found to respond only with sodium chloride. With sodium chloride there was an increase in response with the concentration as in type 'a' hairs. These observations were in agreement with the findings of Hodgson and Roeder (1956) in blowfly labellar hairs. According to Beidler (1954) the increased responses to increasing concentrations might be due to the fact that the magnitude of differential responses in mammalian salt receptor was directly related to the number of ions or molecules reacting with the receptors. The characteristic feature in these studies was the maximal initial response in sodium chloride which decreased in the successive intervals, unlike in type 'a' hairs. The higher initial response suggests the possibility that the sensory pegs possess quick permeability for the test solutions.

In lower concentrations of sodium chloride (0.1 M, 0.25 M and 0.5 M) where the initial response was relatively less the receptors seem to attempt for a quicker adaptation from the first interval itself. On the other hand at a higher

concentration (1.0 M.) where the initial response was much higher the adaptation seem to be a slow process to start with. But after the second interval it was a rapid process. Thus the rate at which the receptor seem to adapt depends on the strength of the stimulus applied. In regard to the adaptation a contrast was noticed between the sensory pegs and type 'a' hairs where in the latter the trend for adaptation was not as clear as in the pegs.

With the sugars examined the sensory pegs exhibited responses of different magnitudes from complete unresponsiveness to fairly good sensitivity as in 'a' hairs of pedipalps. In 'a' hairs responses were elicited from both 'S' and 'L' fibres. But in the pegs the 'L' fibre activity was totally inhibited. The 'S' fibre could not be stimulated with D-galactose, inosital and mannose while it exhibited varying degrees of responses with glucose, sucrose, lactose and raffinose. The maximal response was observed with glucose (monosaccharide) and minimal responses with raffinose (Trisaccharide) (Fig. 12). These results were partly in agreement with the behavioural tests on blowfly Phormia regina, by Dethier (1955a). His tests revealed a spectrum of activity ranging from complete un-responsiveness to extreme sensitivity in the different carbohydrates. Dethier (1955a) tried to correlate these responses with the structural configuration of a sugar. He concluded that the structural configuration of a sugar is most important determinant as an effective stimulus. Dethier (1956) tentatively proposed that the mechanism of stimulation

involved a combination of the sugar molecule with the specific receptor site or substance by weak forces to form a complex which depolarises the membrane after which (or simultaneously) the sugar is removed passively by a shift in concentration gradient. D-galactose, inositol and mannose were found to be non-stimulating on the sensory pegs of the scorpion and these findings were in agreement with Takeda (1961).

The responses in sensory pegs also differ from 'a' hairs in another respect. The pegs exhibited an initial higher response with all the stimulating sugars which decreased in the successive intervals. In 'a' hairs the trend was some what different. The higher initial response in the sugars indicates a rapid permeability of the peg membranes. Receptors subjected to weaker stimulus tend to adapt quickly. The receptors subjected to stronger stimulus were slow in adapting.

Among the amino acids tested the sensory pegs exhibited maximal response with glycine with a simple structural configuration. And the response exhibited with glycine was as high as in 'a' hairs. There was a total inhibition of response in the pegs with amino-butyric acid, tyrosine and arginine while the 'a' hairs elicited good response with aminobutyric acid. There was a partial inhibition in the spike frequency with serine, glutamic acid, aspartic acid and histidine. With glutamic acid the 'a' hairs exhibited good response. With histidine responses were partially inhibited in the sensory pegs as in type 'a' hairs.

These responses were neither in agreement with Hodgson (1952b), Case and Gwillian (1961), who reported that the receptors in cray-fish and crabs were more senstive to amino acids especially to glutamic acid. Nor were these results in full agreement with Case (1964) who demonstrated the existance of dactyloamino acid receptors in the Cancer productus and C.antennarius. He found that DL-L-amino-K-butyric acid, aurine, L-glutamic acid and serine to be more effective in stimulating in the descending order. There was a total or partial inhibition of responses with the different amino acids in the present investigation (ofcourse except in glycine). Laverack (1963) reported that he was unable to detect responses to amino acids in the European Carcinus

The Cockroaches comprise an important menue for the scorpions among the insects on which they feed. Therefore, the responses elicited by the sensory pegs with the "Cockroach shake water" probably has definit significance in their feeding behaviour.

Reddy (1965) suggested that the sensory pegs were associated with the absorption of moisture, which according to him was the major function of the pectine. He further stated that the peg sense organs being numerous in number can absorb significant amount of moisture. The nigh and rapid permeability of the sensory pegs as shown in the present studies further strengthens the openion held by Reddy (1965).

The sensory pegs and the immediately surrounding sensory area of the pectinal teeth when exposed to vapours of xylene, benzene and toluene, elicited responses of varying degrees. Roys (1954) also observed similar electrical activity in cockroaches on exposing the appendages to xylene, benzene and toluene vapours. In his opinion the increased responses recorded from the appendages might be attributed to a specialized chemosensory mechanism. But Hodgson and Roeder (1956) did not agree with the conclusions of Roys. They felt that the effect cannot be attributed to the specialized chemosensory mechanism, but illustrated as due to general irritability of nervous tissue when treated with many chemicals. However, in the scorpion similar effects were not produced when other appendages possessing contact chemoreceptors like 'a' hairs were exposed to such vapours. Therefore, the responses recorded from the pectinal nerve hints at the possibility that by virtue of the presence of the highly permeable sensory pegs on the pectinal teeth the pectin might play an important role in the olfactory reception, although it can not be claimed as conclusive evidence.

On being stimulated with a horse tail bristle the sensory pegs elicited responses in the form of a stream of small spikes. When the same pegs were stimulated by a fine metal pin at frequencies of 15, 60, and 120 CPS responses of varying degrees were recorded. With the increased frequency of stimulus the increase in spike frequency and the production of more than

one spike unit indicates some behavioural significance in the life of scorpion.

When the 'b' hairs were moved with a needle spike units of more than one type were recorded depending on the pressure applied (Fig. a). It appears that the increasing pressure on the hairs resulted in their increasing displacement from their original position. Thus a possible relationship seem to exist between the increasing displacement of the hairs and the spike heights produced. From an earlier study Hodgson and Roeder (1956) reported similar relationship in the labellar hairs of blowfly. By applying a certain mechanical stimulus to the labellar hair they observed at least two types of spike units which were disignated as 'L' and 'S' depending on the heights. In their openion the 'L' and 'S' spikes were produced by different fibres (L and S fibres) and that the 'L' fibre responds to a larger displacement of the hair, while the 'S' fibre responds for shorter displacement. They also expressed that the 'L' fibre responds only after bending of the hair approximately twice the amount necessary to stimulate the 'S' fibre. The white stiff hairs were also shown to respond to the mechanical stimulus (Fig. b).

The responses of the pectine to puffs of air (Fig. c) and continuous streams of air (Fig. d) suggest that the surface sensory structures of pectine might serve to perceive the differences in the wind currents. In cockroach when the cercal hairs were stimulated with a puff of air the evasion response was recorded. But this kind of response was not well

developed among Locusts (as cited by Dethier 1963). Cloudsley-Thompson (1955) from his experiments with the tuning fork suggested that the main role of the pectines of the scorpions lies in the pereeption of ground vibrations. According to him probably they are used more for warning of danger than in detecting the prey.

Thus from the foregone account the pectines appear to serve several functions and all the earlier controversies about the functions of the pectine have resulted from too narrow a concept of the sensory role of the pectines. It is apparent that the possession of the long and stiff hairs enables the pectine to detect mechanical stimulus from the substratum. The pectinal teeth are very important structures in view of the localization of the sensory pegs. The pegs are highly permeable (Reddy 1965) and are responsive to chemical stimulation characters most essential for serving both as hygroceptors and olfactory receptors. Such a role of the pectines had been visualized in courtship and mating behaviour of the scorpions (Gopalakrishna Reddy 1967). Further these sensilla have also been shown, in the present study, to be extremely sensitive to even minute mechanical stimulus and would therefore be capable of sensing the texture of the substratum, a role indicated for them by Alexander (1957). The present results confirm the studies of Hoffmann (1964) on the vibration sensitivity of these pegs. Therefore, the sensory pegs are not only hygroceptive and olfactory in function but also mechano-receptive.

The pectine is thus a complex sensory appendage serving several vital functions in the life of scorpion.

SUMMARY

1. The pectines are a pair of appendages situated ventrally on the second mesosomia in scorpion M.fulvipes, and are provided with sensilla like the sensory pegs, 'b' type hairs and white stiff hairs.

2. The chemo and mechanoresponses of the pectinal sensilla were studied with inorganic salts, sugars, amino acids and different mechanical stimuli.

3. The responses show that the peg sensilla could detect still lesser number of inorganic salts than 'a' hairs on pedipalps while there was not much difference between both in regard to the sugars and amino acids.

4. When tested with the different sugars although the 'S' fibres elicited responses like 'a' hairs there was a total inhibition of the 'L' fibre activity. The sensitivity was in the descending order from glucose, sucrose, lactose and raffinose.

5. Among the amino acids tested fairly good responses were recorded in glycine alone on par with 'a' hairs while in serine, glutamic acid, aspartic acid and histidine the magnitude of response was much less than in 'a' hairs.

6. The initial higher responses in all these tests lend further support to the opinion held by earlier workers that the pegs due to their high permeable nature probably serve as hygroceptors and olfactory receptors.

7. By virtue of the location of different sensilla the pectine seem to perceive the mechanical stimulus from diverse sources including the variations in the wind currents. Thus the pectin is a complex structure supposed to be a hygroceptor, olfactory receptor and mechano receptor. Evidence indicates that the pectin is of a lesser nature of contact chemoreceptor.

CHAPTER III

VIBRATION RECEPTORS IN THE WALKING LEG

INTRODUCTION

Yet in none of these studies the functions of these sensilla were properly assessed. Millot (1949) believed that the slit sense organs were chemoreceptors, an openion already held by McIndoo (1911) and Keston (1935). Using electrophsiological techniques Pringle (1955) showed that the slit sensilla in the scorpion H. (Palamneus) swammerdami, are mechanoreceptors analogous to the campaniform sensilla of insects. Walcott and Van Der Kloot (1959) reported the presence of vibration receptors(mechano-receptors)located on the legs of web spinning spider Achaearanea tepidoriorum.

In a preliminary survey carried out in the scorpion H. fulvipes, two sensilla were seen each located at different points on the same walking leg. One of them was seen in the joint between the first and second tarsomeres and the other at the base of the terminal claw. Among these the former responds for low frequency vibration and the latter for high frequency vibration. It is with this background that an attempt was made to extend these studies further to evaluate the functions of these vibration receptors using the modern electrophysiological techniques.

MATERIAL AND METHODS

The walking leg of the scorpion, H. fulvipes, was the experimental material in the study of the vibration receptor. The rearing of the experimental animals in the laboratory, and other details were the same as mentioned in the earlier chapter.

In arthropods the appendages play an important role in the perception of the surroundings. Therefore, most of the sensilla are shifted on to the appendages. Venkateswararao (1963) gave a detailed description of the sensory structures on the appendages in H. fulvipes. The first and second tarsomeres which come in direct contact with substratum are furnished with the largest number of sensory bristles. Both the podomeres are devoid of musculature and are filled with connective tissue traversed by innumerable nerve twigs. In the whole of the ambulatory leg it is only the distal tip of the second tarsomere that is equipped with epidermal and subepidermal ganglia and the solitary neurosomata. The slit sensilla are located between the first and second tarsomeres very close to the neurosomata (Fig. 4). In surface view the sensilla appear as shown in Pm. 5. They are less in number often concentrated into groups. Examination of this area (between first and second tarsomeres) under a compound microscope revealed that each group consists of nine transverse grooves one below the other. Of the nine slit sensilla the central ones are the largest planked on either sides by smaller ones. What appears as a slit in surface view is just the

Legends for figures

Figs. 3 and 4. Anterior and posterior view of the fourth walking leg of scorpion *H. fulvipes*, respectively.

Cx - Coxa; Tr - Trochanter; Fm - Femur; Pat - Patella; Tb - Tibia; T1 - Tarsus 1; T2 - Tarsus 2; U - Unguis or claw; T1 - T2- Joint between tarsus 1 and tarsus 2 (Note the location of the slit sensilla at the joint in the ventral view (Fig. 4)

b - 'b' hairs; c - 'c' hairs.

Pm. 5. Photomicrograph to show the external appearance of some of the grooves in the slit sensilla. Note the dilation in the center of the groove with a characteristic appearance around the slit and the gradation in the size of the grooves.

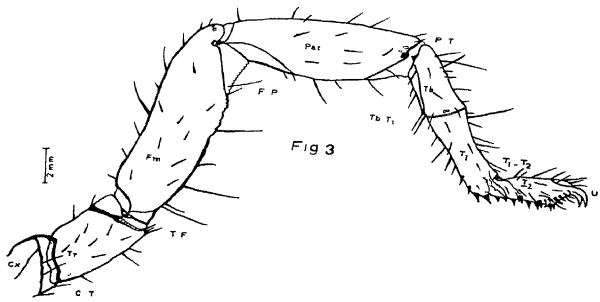

Pat
P T
F P
Fm
Tb T1
T1
T1 - T2
T2
T F
Cx
T T
C T

Fig 3

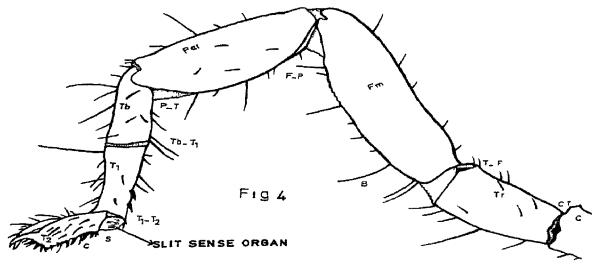
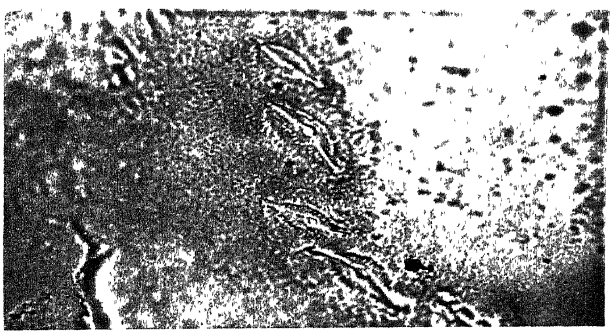

Pat
F-P
Fm
Tb
P-T
Tb-T1
T1
T1-T2
T-F
T1
C T
C
S
SLIT SENSE ORGAN

Fig 4



thinned out cuticle surrounded by a cuticle slightly more pronounced than the usual.

Methods

Location of the receptor site:

It is a common experience that the scorpion alerts itself by mere tapping of the substratum on which it rests. During the current electrophysiological studies of the vibration sensilla on the leg of a scorpion it was found that the nerve action potentials could be elicited by a mere tap on the table. Further study disclosed that the receptor responsible for this vibration senstivity was located somwhere on the leg. To locate the receptor more precisely recordings were made from the leg nerve forcibly vibrating the podomeres at different levels by means of a fine needle mounted on a crystal phonograph cartridge. In the process it was revealed that a crucial portion between the first and second tarsomeres has the ability to respond to low frequency vibrations ranging from 15 to 200 cycles per second (CPS). This crucial region exhibiting the ability to respond to the above frequency range is the spot occupied by the slit sensilla.

When the needle of the crystal phonograph cartridge was passed on to the base of the terminal claw of the walking leg it responded to high frequency vibrations ranging from 400 to 14,000 CPS. Probably this spot represents the high frequency vibration receptor. Thus in scorpion the vibration

receptors are located at two different regions on the same walking leg. These findings were confirmed by repeating similar tests on 20 preparations, of different sizes and sex.

Low frequency vibration receptor:

In order to study the low frequency vibration responses the walking leg of an anesthetized scorpion was amputated at the trochanter-femur joint. The proximal end was pinned to a cork so that the distal end of the leg protruded freely over the edge. The cut end was kept in a small trough containing fresh scorpion ringer solution and an Ag-AgCl electrode was placed in this pool of ringer's. Another Ag-AgCl electrode was inserted through the cuticle of the patella joint. The electrodes were connected to the cathode follower input of an AC coupled pre-amplifier. The output from the pre-amplifier was connected to the Oscilloscope (Philips GM3156). The fine needle of the Crystal Phonograph cartridge (5.2 Ronette, S.A.250, SA:100) was positioned carefully above the slit sense organ such that during vibration the needle compresses the thin membrane of the sense organ. The other end of the crystal phonograph cartridge was in turn connected to the stimulator for low frequencies.

When certain pressure was carefully applied to the slit sense organ through the fine needle of a crystal phonograph cartridge which in its turn was activated by the stimulator, the sensilla was compressed and thus stimulated. The action potentials displayed on Cathods Ray Oscilloscope screen were

photographically recorded on 35mm film by Oscillographic Camera (Philips Voigtlander). Visual counts of the spikes were made from identical records. It was observed that the displacement of the needle of the crystal phonograph cartridge was approximately proportional to the applied voltage. Olson (1957) and Walcott and Van Der Kloot (1959) reported similar properties for the crystals they studied. The crystal phonograph cartridge was functioning efficiently within the voltages and frequencies applied in the present investigation.

The slit sensilla were compressed at 15, 28, 30, 60, 80 100 and 200 CPS in the low frequency range, altering the strength of the stimulus from one to twenty volts. Care was taken that the position of the receptor at which the initial stimulus was applied was not altered during the successive stimuli over the above frequency range. The responses of the sensilla in the entire frequency range changing the stimulus were recorded in the same preperation. The recording was repeated on four preparations. Responses were recorded continuously and the data were analysed for intervals of five seconds each.

<u>High frequency vibration receptor:</u>

From the preliminary survey it was observed that the vibration receptor located at the base of the terminal claw of the walking leg of the scorpion <u>H. fulvipes</u>, responds to the high frequency vibration. The general experimental set up and other details not mentioned here are the same as reported for low frequency vibration.

The tip of the claw was attached to the fine pin which in its turn was attached to the diaphragm of the microphone. The microphone was connected with the Audio-Oscillator. The other end of the amputated leg was connected with Ag-AgCl electrodes which in turn were connected to the input of the pre-amplifier. The output of the pre-amplifier was connected to the oscilloscope (Philips GM 3156).

The microphone (Japan, 2.5" diameter and 0.1 W) was calibrated with the help of a standard condenser microphone cartridge type - 4131 - Briiel & Kjaer, Beat frequency Oscillator, type 1011 - Briiel & Kjaer and audio-frequency spectrometer. The calibrated values are arbitrary and were reported in the accompanying graph (Plate 5 fig. 20a). The microphone was working perfectly between the frequencies 400 to 18,000 CPS. Resonance of the microphone does not effect the impulses. In these studies only the frequencies but not the intensity or amplitude were measured.

To minimise the influence of temperature variations and external air borne disturbances on the receptor activity the whole experimental set up for the study of low and high frequency vibration reception was arranged in an air-conditioned chamber in a wire-mesh case at a temperature of 22 $\pm$ 2° C.

The responses of the high frequency vibration receptor were recorded at several frequencies in the range of 400 to 14,000 CPS raising the stimulus from one volt, its threshold.

Care was taken not to disturb the initial set up of the receptor during successive tests. The responses for the entire high frequency range could not be recorded on a single preparation because the time involved was too long. Therefore, the frequency range from 400 to 2,000 CPS was recorded in one preparation and the range 2,400 to 14,000 CPS in a second preparation. Usually the receptor took a maximum of 2 minutes to recover after each stimulus. Hence 3 minutes recovery period was allowed between successive tests. Recordings were made on four sets of preparation at each stimulus.

Each record was counted thrice and the final averages of spike counts of the reproduciable records of the four sets of preparations were tabulated for intervals of first, fifth and tenth half seconds. Individual variations in the spike count between preparations were reported.

RESULTS

Threshold:

The threshold of the vibration receptor of the scorpion leg was measured. Electrodes were inserted into the amputated leg. The needle of the crystal phonograph cartridge was carefully positioned over the slit sense organ. To determine the threshold of a preparation at a given frequency the strength of the stimulus (in volts) was increased at a uniform rate until a change was detected in the rate at which the action potentials were recorded from the leg. The minimum strength of stimulus necessary to cause a change in the rate of action potentials was defined as the threshold. In the present study the threshold value was one volt at a frequency of 15 CPS.

In a range of 15 to 14,000 CPS in which the receptor was responding the threshold varied with the frequency. In the low frequency range of 15 to 200 CPS the variation was more. In a frequency range of 15 to 100 CPS the threshold varied from one to two volts. Similarly between 100 to 200 CPS the threshold changed from two to four volts, for a change of 100 CPS in frequency (Figs. 16A to E). In the high frequency range the nerve fibres producing spike units A, B, C, D and E were responding over a longer duration in the entire range (400 to 14,000 CPS) so long the stimulus strength was maintained at one volt, its threshold. Once the stimulus strength was increased to two volts two problems were noticed. In the first place the fibres producing spike units A and B were alone responding at the higher stimulus (Fig. 26). Secondly

Legends for plate 3.

Figs. 15 to 19. Responses from the slit sensilla in scorpion H. fulvipes, at different frequencies and stimuli.

Figs. 15A and B. Number of impulses per second at frequencies of 60 and 100 CPS respectively, plotted separately against time in seconds to compare their responses at 6 and 10 Volts stimulus strength.

Figs. 16A to E. Number of impulses per intervals of five seconds each, at frequencies 15, 28, 60, 100 and 290 CPS respectively, plotted separately against increasing stimuli to show that the rate of activity decreases on stimulating the receptor successively under identical conditions.

Lines with closed circles (•-•-•-•) represent responses recorded in the first intervals, open circles (o-o-o) in the second intervals, open triangles (Δ-Δ-Δ) in the third intervals and with multiplication marks (x-x-x) in the fourth intervals.

Figs. 17 and 18. Number of impulses per intervals of five seconds each, at different stimuli (1, 6, 10 and 15 volts) were plotted against increasing frequency range to show that at 28 CPS higher responses were noticed at all the stimuli tested.

Fig. 19. Number of impulses per intervals of five seconds each, recorded at different frequencies were plotted against stimulus strength to show the relation between the responses at the frequencies and the strength of the stimulus (voltages).

PLATE-3

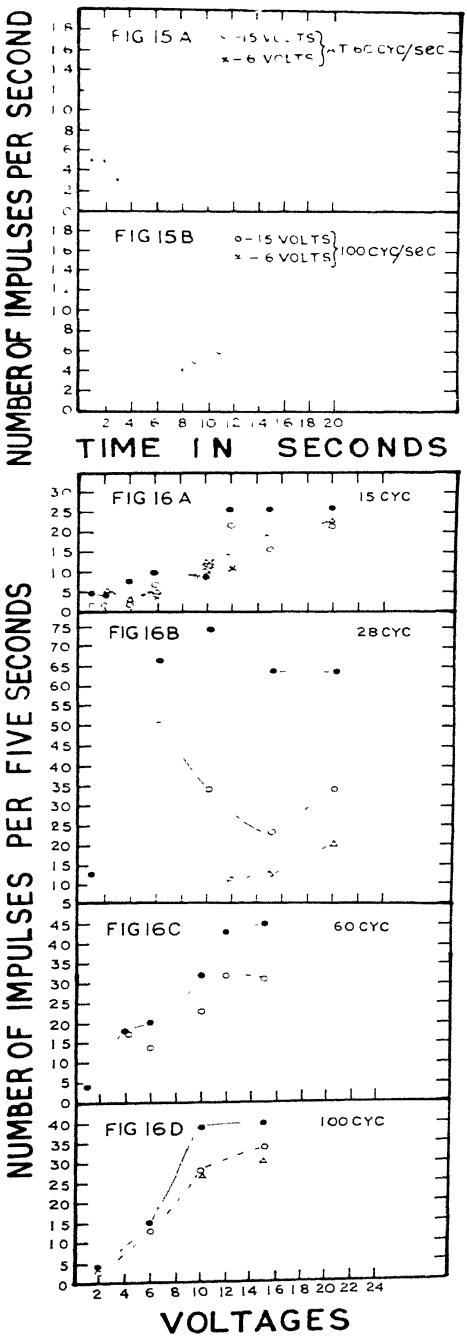


FIG 15 A
o – 15 VOLTS
x – 6 VOLTS
AT 60 CYC/sec
FIG 15 B
o – 15 VOLTS
x – 6 VOLTS
100 CYC/sec
NUMBER OF IMPULSES PER SECOND
TIME IN SECONDS
FIG 16 A
15 CYC
FIG 16 B
28 CYC
FIG 16 C
60 CYC
FIG 16 D
100 CYC
NUMBER OF IMPULSES PER FIVE SECONDS
VOLTAGES

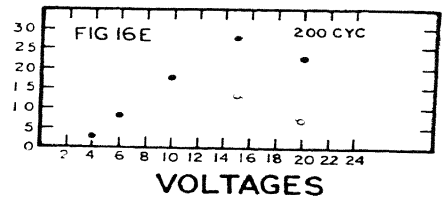


FIG 16 E
200 CYC
VOLTAGES

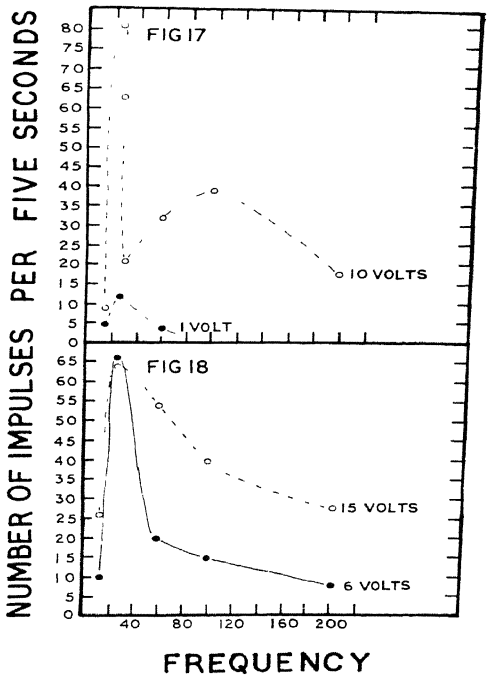


FIG 17
10 VOLTS
1 VOLT
FIG 18
15 VOLTS
6 VOLTS
NUMBER OF IMPULSES PER FIVE SECONDS
FREQUENCY

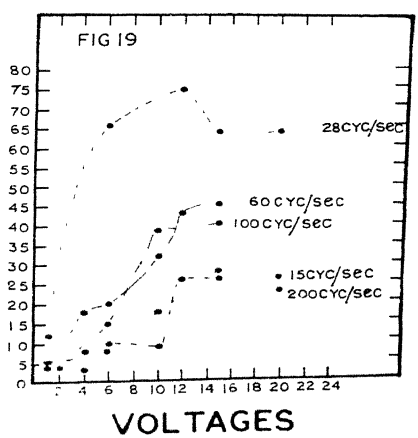


FIG 19
28 CYC/sec
60 CYC/sec
100 CYC/sec
15 CYC/sec
200 CYC/sec
VOLTAGES

the duration of the firing from the fibres producing spike unit 'B' was very short, i.e., about 4 seconds only although fibres producing spike unit 'A' responded as they did at one volt.

Responses from slit sensilla

The responses of the sensilla were recorded in a frequency range of 15 to 200 CPS at 1, 2, 4, 6, 10, 12, 15, and 20 volts stimulus strength and the ummber of impulses for intervals of five seconds each at different frequencies were plotted against the increasing stimulus (Fig. 19). The receptor did not respond for frequencies below 15 CPS and above 200 CPS at any stimulus strength, indicating that these are the lower and upper limits of responses of the slit sensilla. At both the frequencies of 15 and 200 CPS the action potentials were lowest (Fig. 19). At 200 CPS the stimulus had to be raised to four volts to obtain a response. Attempts were failed to get any responses at frequencies of 30 and 80 CPS in the entire stimulus range. Only moderate responses were recorded at frequencies 60 and 100 CPS. The receptor was highly sensitive at 28 CPS over a wide range of stimulus (Figs. 17 and 18).

The action potentials were seen to increase with increasing stimulus strength in a range of 1 to 20 volts. But in a range of 6 to 15 volts (Fig. 19) the receptor was performing much better than at other stimuli. The action potentials were either decreased or totally stopped beyond the range of

6 to 15 volts (Fig. 19). Beyond 20 volts the receptor ceased to respond totally at any frequency.

Responses from high frequency vibration receptor:

Attempts were made to study the responses of the high frequency vibration receptor, by direct vibration, at different frequencies in the range of 400 to 14,000 CPS increasing the strength of the stimulus from one volt, its threshold value. It was noticed that 400 and 14,000 CPS were the lower and upper limits of response of the receptor. The receptor ceased to respond totally beyond a stimulus strength of two volts.

All the action potentials recorded from the receptor were not of the same height. The analysis revealed spikes of at least five different heights ('A', 'B', 'C', 'D', and 'E', and 15μV, 20μV, 25μV, 30μV, 50μV, respectively). In view of the very high spike frequency exhibited by the receptor, the impulses for the first, fifth and tenth half second intervals were alone taken. The number of impulses for each interval were plotted on a single log-graph sheet against the frequency at a given stimulus. Seperate graphs were made for each spike unit (Fig. 21 to 26).

With the change of frequency of vibration in the range of 400 to 14,000 CPS corresponding variations were observed in the responses of the nerve fibres. The differences in the spike heights might be due to the inherent property of nerve fibres of the vibration receptor (Walcott and Van Der Kloot 1959).

Legends for plate 4.

Figs. 21 to 26. Responses from the high frequency vibration receptor in scorpion *H. fulvipes*, at different frequencies and stimuli.

Number of impulses for the first, fifth and tenth half seconds were plotted on semi-log graph sheets separately against the frequency (CPS) at one volt (Figs. 21 to 25) and at two volts (Fig. 26) to show that different nerve fibres producing spike units A, B, C, D and E (Figs. 21 to 25 respectively) exhibit optimal activity at different frequency ranges. In fig. 26, spike units A and B were alone recorded.

Lines with closed circles (•-•-•) represent responses in the entire frequency range during the first half seconds, multiplication marks (x-x-x) fifth half seconds, triangles (▲-▲-▲) tenth half seconds and open circles (o-o-o) represent 'B' spike unit in fig. 26.

PLATE-4

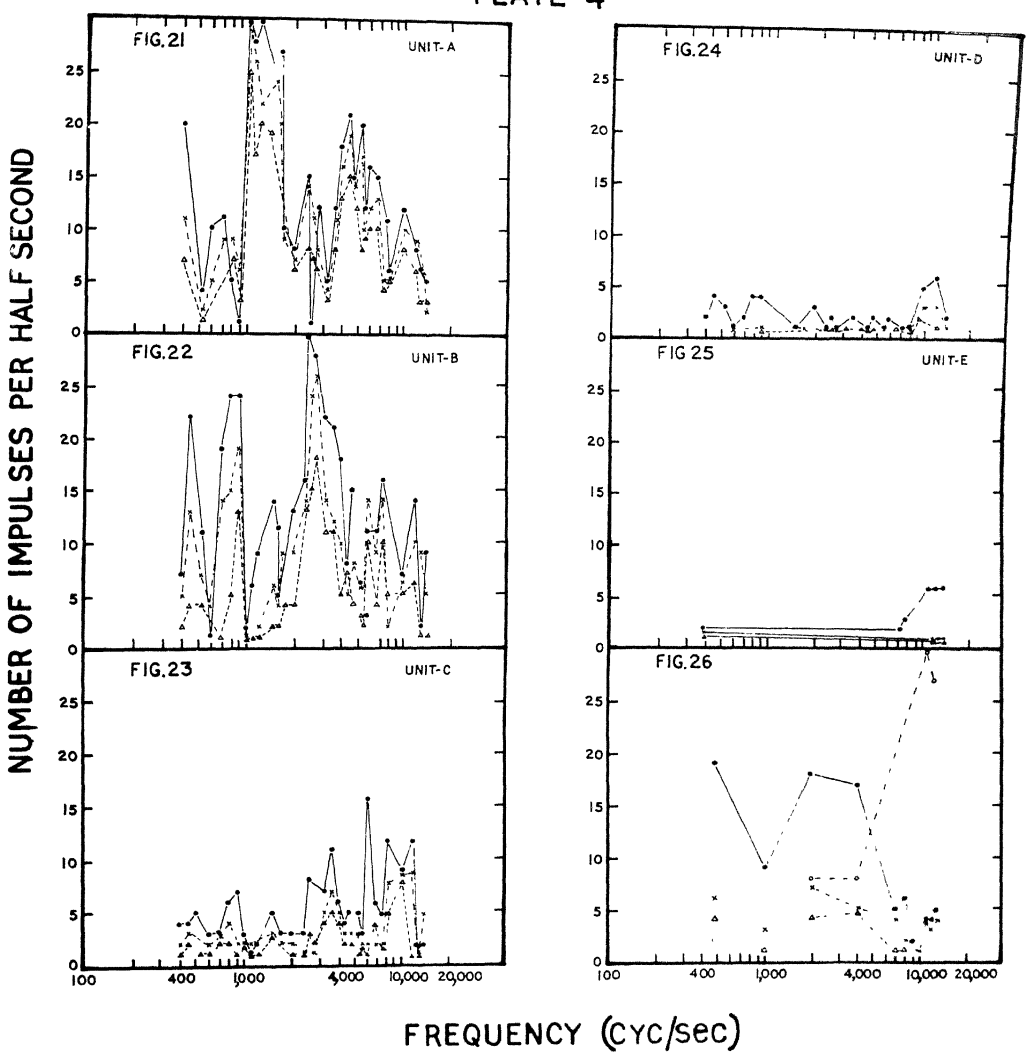


FIG. 21
UNIT-A
FIG. 22
UNIT-B
FIG. 23
UNIT-C
FIG. 24
UNIT-D
FIG 25
UNIT-E
FIG. 26
NUMBER OF IMPULSES PER HALF SECOND
0
5
10
15
20
25
100
400
1,000
4,000
10,000
20,000
FREQUENCY (CYC/sec)

The fibres producing five types of spikes were responding throughout the frequency range tested. But it appears that each fibre or group of fibres producing spikes of a particular height were showing maximal responses in a certain frequency range (Figs. 21 to 25). Thus the fibre or fibres responsible for the production of unit 'A' spikes responded maximally between 1,000 to 1,600 CPS (Fig. 21); of unit 'B' spikes responded maximally between 2,400 to 4,000 CPS (Fig. 22); of unit 'C' spikes responded maximally between 6,000 to 12,000 CPS (Fig. 23) and of unit 'D' spikes responded maximally between 9,000 to 14,000 CPS (Fig. 24). The fibres producing the unit 'E' spikes elicited least responses over a wide range (From 500 to 7,500 CPS), They exhibited slightly higher responses between 8,000 to 14,000 CPS during the first half second only (Fig. 25).

Further the responses of the vibration receptor were studied in the same frequency range increasing the voltage from one to two. The fibres responsible for the production of 'A' unit spikes responded maximally between 2,000 to 4,000 CPS. Fibres producing 'B' type unit spikes responded maximally beyond 4,000 and up to 12,000 CPS (Fig. 26). The fibres responsible for the production of type 'C', 'D', and 'E' spikes ceased to respond at this voltage.

Adaptation:

The number of impulses at different frequencies during intervals of five, ten fifteen and twenty seconds were plotted separately against the stimulus strength (Figs. 16A to E). The

duration of the nerve discharge varied with the frequency applied under identical stimulus. At lower frequencies (15, 28 CPS) the receptor elicited responses for a longer duration of 20 and 15 seconds respectively (Figs. 16A and B). With a progressive increase in the frequency of 60,100 and 200 CPS the duration for which the receptor responded decreased gradually (Figs. 16 C, D, and E).

The fact that the action potentials decreased in the successive intervals at the different frequencies indicates that the receptor exhibited a tendency towards adaptation. when the number of impulses obtained at 60 and 100 CPS were compared separately (Figs. 15 A and B) at stimuli of 6 and 15 volts against time a similar trend for adaptation was noticed in the receptor. It was also shown that fibres producing an initial higher spike frequency at a higher stimulus (15 volts) exhibited a tendency for a comparatively quicker rate of adaptation than at a lower stimulus (6 volts).

The spike frequency elicited by the high frequency vibration receptor in the first, fifth and tenth half second intervals at a strength of one volt were plotted against the different frequencies applied (Figs. 21 to 25). A comparison of the responses during the successive intervals showed a gradual decrease in the spike count which indicates an attempt for adaptation. A similar trend was clearly seen from the same receptor when stimulated with a higher strength of 2 volts (Fig. 26). But at 2 volts similar attempt for adaptation was

Legends for films

Films to show the responses recorded from the slit sensille on the walking leg of scorpion *H. fulvipes*, at the following frequencies (in the low frequency range) and stimuli.

A. Responses at 15 CPS and 1 Volt.

B. Responses at 15 CPS and 12 volts.

C. Responses at 25 CPS and 1 volt.

D. Responses at 28 CPS and 15 volts.

E. Responses at 100 CPS and 2 Volts.

F. Responses at 100 CPS and 10 Volts.

G. Responses at 200 CPS and 4 volts.

H. Responses at 200 CPS and 15 Volts.

A
B
C
D
E
F
G
H

noticed only in the fibres producing spike unit, A. The fibres producing spike unit B responded only for a very short duration and the time interval was not sufficient to notice any trend for adaptation.

Latency:

The latency is the time delay between the application of the sine wave pulse to the microphone and the first action potential recorded from the nerve. In the present study by direct vibration of the leg the latency includes the time necessary to set the leg tip vibrating (this includes the latency in the microphone), the time necessary to excite the receptor and finally the conduction time to the nerve and to the electrodes. This time delay was measured from the photographs taken from the Oscillograph. From the speed of the films the latency time was calculated. The latencies were determined for several frequencies of stimulation in the high frequency range. The latency time taken at each frequency (in milli-seconds) was plotted in a graph against the frequencies.

The measurements showed that the latency varied with frequency of sound stimulus. From the graph (Fig. 20b) it was seen that the latency decreased with the increase in the frequency of vibration. At 400 CPS while the latency was 18 milli-seconds it was only 2.5 milli-seconds as the frequency was increased to 14,000 CPS. These observations were in agreement with Walcott and Van Der Kloot (1959) who studied the latency time for the air borne sound vibrations.

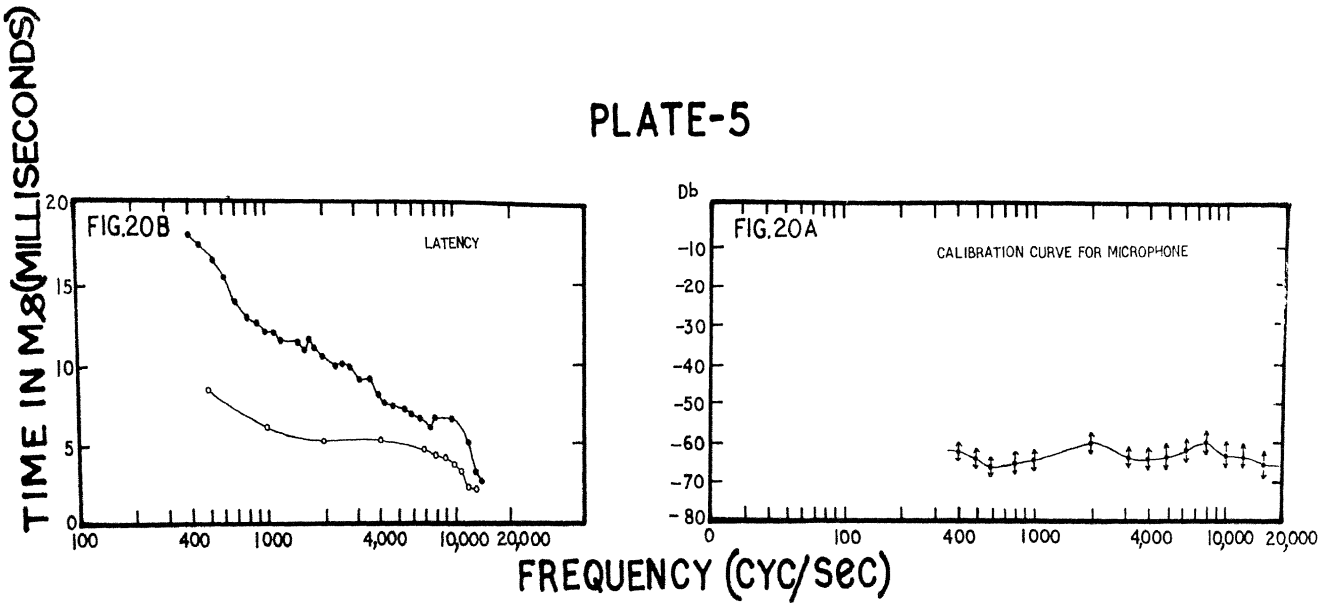
Legends for plate 5.

Fig. A: Calibration curve of the microphone (Japan, 2.5 diameter and 6.1 W).

Fig. B: Latency time in milliseconds calculated for high frequency vibration reception plotted against the frequency (CPS)

Closed circles (•—•—•) at one volt stimulus; open circle (o-o-o) at two volts stimulus.

PLATE-5


TIME IN MS(MILLISECONDS)
FIG.20B
LATENCY
20
15
10
5
0
100
400
1000
4,000
10,000
20,000
Db
FIG.20A
CALIBRATION CURVE FOR MICROPHONE
-10
-20
-30
-40
-50
-60
-70
-80
0
100
400
1000
4,000
10,000
20,000
FREQUENCY (CYC/SEC)

In the present investigation no after discharge was found on stimulating the low and high frequency vibration receptors directly.

DISCUSSION

It was shown that the scorpion H.fulvipes, has sensitive vibration receptors located in two regions on the walking legs. The location of the vibration receptor on the legs is not a strange phenomenon exclusive for scorpions. Earlier studies revealed that the location of both hearing and vibration sensitivity in the legs is quite common among the insects (Autrum 1941, Autrum and Schneider 1948, Imms 1957) and spiders (Walcott and Van Der Kloot 1959).

The scorpion is sensitive for a wide range of frequency. Under experimental conditions both the vibration receptors responded separately for a frequency range of 15 to 200 CPS (low frequency) and 400 to 14,000 CPS (high frequency). The frequency range in which the scorpions responds was not as large as that reported for several spiders and insects. The spider is sensitive to sounds (air borne) of a frequency range from below 20 to 45,000 CPS (Walcott and Van Der Kloot 1959). The noctuid moth is sensitive to sounds from 2,000 to 2,00,000 CPS or more (Roeder and Treat 1957), the Acrididae (Haskell 1956) from 100 to 20,000 CPS, the Gryllus (Pumphery and Rawdon-Smith 1936C) 50 to 10,000 CPS and Locusta 300 to 10,000 CPS.

The unusual feature of the scorpion vibration receptor is the location of each of the two sensilla, capable of responding to two different frequency ranges, at distinct regions on the same walking leg. The slit sensilla responds in a frequency range of 15 to 200 CPS while the receptor located at the claw responds in a range of 400 to 14,000 CPS.

The slit sensilla seem to perform well under certain set conditions. The threshold of the sensilla varied with the frequency of the vibration. At 15, 28 and 60 CPS the threshold was one volt, while at 100 and 200 CPS it increased to 2 and 4 volts respectively. Other conditions being identical there was an increase in the rate of spike frequency with increase in the stimulus strength. But it was observed within a certain range of voltage. The sensilla responded fairly well between 6 to 15 volts. While experimenting with the second order neuron of cat ear Galambos and Davis (1943) found a similarly increased rate of nerve discharge proportional to the sound pressure. The findings of Walcott and Van Der Kloot (1959) were also in agreement with the present observations. In the vibration receptor of spider Achaearaea tepidariorum, they found increased responses in a range from the threshold to 20 db above the threshold sound pressure.

In the present experiments when once the stimulus strength was increased beyond 15 volts the action potentials were either decreased (at 15, 28, and 200 CPS) or totally stopped (at 60 and 100 CPS). The slit sensilla failed to respond at any frequency once the stimulus was raised above 20 volts. In fact it was a surprise that beyond a certain stimulus strength the sensilla exhibited either decreased responses or a total failure. From a comparative study of responses of vibration sensilla of an intact and isolated leg of spider A. tepidariorum, Walcott and Van Der Kloot (1959) concluded that the

cause for the decrease in the rate of nerve discharge with the increase in the strength of the stimulus was an artifact caused by isolating the leg.

Under identical conditions of stimulus the sensilla responded maximally at 28 CPS and minimally at 15 and 200 CPS. The response was median at 60 and 100 CPS while at 30 and 80 CPS there was none at all. Thus depending upon the frequency the sensilla was observed to exhibit responses of varying degrees. The diferrential responses might be due to the sharp selectivity of the receptors between frequencies. In spider A.tepidariorum, Walcott and Van Der Kloot (1959) found that the effective frequencies of responses were clearly defined. In spiders while the receptors responded clearly at 30.5 Kc, there was none at 30.0 Kc, or 30.4 Kc. In their opinion the frequency of sensitivity to direct vibration of the lamella seem to be a constant property of the receptor.

Under the same stimulus the duration of firing from the sensilla varied with the frequency applied. There was a gradual decrease in the duration of response obtained from a receptor with the progressive increase in the frequencies from 15 to 200 CPS (Figs. 16A to E). Thus under the conditions of study the slit sensilla appear to be oriented to respond for a longer duration at low frequency vibrations (15 and 28 CPS) while at high frequency vibrations (100 and 200 CPS) probably the sensilla get fatigued quickly.

From the foregone account it was clear that the slit sensilla responds well within certain limitation. The

sensilla functions within a specific range of stimulus strength. The optimal performance would be between 6 and 15 volts. The receptor has a lower (15 CPS) and upper (200 CPS) limits of frequency range within which it could respond. In this range the receptor was very sensitive at 28 CPS.

The high frequency vibration receptor functions in a frequency range of 400 to 14,000 CPS at a very weak stimulus of one volt. With an increase in the strength of the stimulus, above threshold fibres, other than those producing spike types A and B, were not responding. The receptor ceased to respond totally above a stimulus of two volts.

Just like the slit sensilla the high frequency vibration receptor also has its lower (400 CPS) and upper (14,000 CPS) frequency range. By vibrating the leg tip directly it was shown that there were differences in the responses of the high frequency vibration receptor from one frequency to another. This was inferred by the production of different spike units (A, B, C, D & E). Further each of these fibres were shown to be highly sensitive in a particular frequency range (Figs. 21 to 25). These results implied that the sense organ is composed of a series of receptors each of which tuned to a specific frequency. A similar result was obtained when the spider leg was tested with air-borne vibrations, by Walcott and Van Der Kloot (1959). But they reported that when the leg tip was

forced to vibrate directly the property of tuning of the individual receptor units of the sense organs was largely lost unlike in the scorpions.

According to Pumphery and Rawdon-Smith (1939) frequency discrimination can be accomplished by either of the three basic mechanisms. One of them is that different fibres may be excited by different frequencies. The mammalian ear has been shown to use the technique of differential fibre response at different frequencies (Galambos and Davis 1943; Tasaki 1954). It is interesting that the spider uses a system of differentially responsive fibres, in many ways analogous to mammalian ear (Walcott and Van Der Kloot 1959). The above system in spiders functions only for air-borne sound between a frequency range of 100 to about 1,000 CPS. Scorpions can discriminate a wide range of frequencies by direct vibration. The range of frequency discrimination was very high when compared with the fibre responses in spiders by direct vibration reported by Walcott and Van Der Kloot (1959).

When the leg tip was directly vibrated it appears that the scorpion could distinguish the frequencies using the technique of differential fibre response at different frequencies. It is not surprising to note that the scorpions with their burrowing mode of life could discriminate the frequencies by direct vibration over such a wide range while the spiders with their aerial mode of life could discriminate so, if the vibrations were air-borne. It was found that receptors in both the

slit sensilla and the high frequency vibration receptors exhibited a tendency towards adaption on being stimulated successively. It was also noticed in the slit sensilla that the greater the strength of the stimulus applied the faster the rate of adaptation. Similar findings were reported by Walcott and Van Der Kloot (1959) in the course of their study on spider vibration receptors. But the results in scropion vibration receptor were in marked contrast to the Orthopteran ear which does not adapt at all. The rate of adaptation in scorpion vibration sensilla is not as fast as in Noctuid. In Noctuid the rate of nerve discharge dropped from a very high initial level of 1,000 per second to an irregular discharge of 90 per second in about 20 seconds (Roeder and Treat 1957). The second order neuron in cat exhibited a much faster rate of adaptation which was virtually complete within 0.1 second (Galambos and Davis 1943).

The slit sense organ by virtue of its location between the first and second tarsomers could be raised above the substratum level during the movements of scorpion as desired. Thus it appears to be suitable for the reception of airborne vibrations too. The fact that it exhibited radical changes in the threshold with slight alteration in frequency, further strengthens this view because the sound waves at certain frequencies are more effective in vibrating the sensilla. In the openion of Walcott and Van Der Kloot (1959) such radical changes in the threshold for slight changes in frequency is a characteristic of the receptor system stimulated by air-borne sounds. The slit sensilla was

shown to consist of nine grooves of varying sizes. It is interesting to verify whether the size differences of these grooves would contribute in the differential responses of the vibration reception.

The high frequency vibration receptor might probably servein the perception of very weak ground borne vibrations. Thus the receptor would warn the scorpion of the slow moving prey or predator.

SUMMARY

1. In the scorpion Heterometrus fulvipes, the vibration receptors are two distinct sensilla, one located between the joint of first and second tarsomeres and the second at the base of the claw on all walking legs. The former (slit-sense organ) responds for low frequency vibration and the latter responds for high frequency vibration.

2. The slit sensilla functions within a stimulus range of 1 to 20 volts. But the high frequency vibration receptor responds only at 1 and 2 volts. In the slit sensilla the threshold of stimulus varied radically with the frequency. In the case of high frequency vibration receptor not only the threshold did not vary in the entire frequency range tested but also the optimal response was elicited at the threshold only. In slit sensilla the optimal responses were noticed in a 6 to 15 volt stimulus range.

3. The slit sensilla responds in a 15 to 200 CPS frequency range while the high frequency vibration receptor responds in a 400 to 14,000 CPS frequency range.

4. The slit sensilla was very sensitive at 28 CPS. The responses from the high frequency receptor showed atleast five spike units A, B, C, D and E, designated thus depending on the spike heights. Each spike unit was supposed to be the product of a specific nerve fibre or set of fibres each of which were responding optimally in a particular range of frequency.

5. When both the sensilla were stimulated successively they were observed to adapt to the stimulus gradually. The slit sensilla were failing to respond for the same duration at all the frequencies. While the sensilla appear to be oriented to respond over a longer duration (~~25~~ seconds) at low frequency (15 and 23 CPS) they seem to get fatigued quickly as the frequencies were increased to 100 and 200 CPS. In the case of the high frequency vibration receptor no such differences, in relation to the duration of response, were noticed in the entire frequency range.

6. Both the vibration receptors were exhibiting responses of varying degrees with the change in the frequency and the differential responses were explained as due to the sharp selectivity of the receptors between frequencies.

7. Thus both the receptors appear to suit the mode of life of the scorpion and help it in perceiving the surroundings.

GENERAL DISCUSSION

Although scorpions have wider distribution, generally they are believed to be characteristic of dry and desert like regions. They are essentially nocturnal animals, spending the day time hiding in nooks, crevices, pits and burrows. Being nocturnal they do not rely much on the sense of vision. To suit their habitat a hard sclerotized cuticle has been developed. This cuticle reduces the water evoperation of the body fluids and also offers more protection to the internal organs in burrowing mode of life. Because of the cuticle the sensitivity to the external conditions is lessened and this is compensated by the development of a multitude of sense organs.

In the evolution of arthropods the appendages are given importance as tools of perception of the surroundings. Thus in scorpion the pedipalps and ambulatary legs of the prosoma are stretched far out from the body and are likely to come in contact with the foreign body first (living or non-living) before any other part of the prosoma. As such most of the sensilla are shifted on to the appendages leaving a few on the body part of the prosoma. This is further illustrated when the distribution of the sensory bristles are studied on the podomeres of the walking legs. Studies by Venkateswararao (1963) showed that the numerical strength of the sensory bristles increases towards the distal end of the limbs which lie in contact with the substratum.

The pedipalp is the second postoral segment of the scorpion. Being chelate they serve as the prehensile organ and intimately associated with the feeding of the animal. Being cactoid it helps in digging and burrowing. The pedipalps are thus all important to the animal. Its behaviour depends to a large extent on its efficiency. Therefore,it is furnished with different types of sensory structures essential for the effeciency. The chemosensory hairs (type 'a') which play a predominent role in the perception of the food organisms are mostly seen on the dorsal surface and lesser on the ventral surface of the hand and fingers. They are rarely seen on the proximal segments. From the foregone studies it was shown that they are the tools in responding to the inorganic and organic environment. The mechanoreceptors ('b' type hairs) are also distributed on the pedipalps although numerically lesser.

The scorpions have little use for their eyes in the nocturnal life except for distinguishing the intensity of light. It is the pedipalp which will perform the role of the eyes perceiving the physicochemical surroundings and convey the message as what is prey and what is predator and what to consume and from what to flee away. The pedipalps are thus not only the physico-chemical eyes of the animal but are also organs of offence and defence.

The pectines are no less important for the scorpion. They are furnished with the large number of sensilla. It is a

a complex and important appendage serving several vital functions. The long and stiff hairs on the pectines ('b' type) enable to detect mechanical stimuli including low frequency substratum borne vibrations. In their mode of life the sensory pegs on the pectines help to absorb the moisture and thus conserve the water balance in the body fluids. Their ventral location do help in absorbing the moisture from the substratum. Reddy (1965) had shown a relationship between the number of sensory pegs and the rate of absorption of moisture between males and females. From the present studies it was found that the sensory pegs showed a higher rate of absorption when compared with the chemosensory 'a' hairs on the pedipalps. The rapid permeability allows them to absorb the maximum amount of moisture content in a given time in their dry habitats as and when the occasion arises. The water is essential to maintain the ion ratio's in the blood and in the metabolic activities. The capacity to detect lesser number of compounds by the pectinal sensory pegs when compared with the chemosensory 'a' hairs on the pedipalps, the lower rate of response and the higher rate of permeability indicate that these are primarily concerned with moisture absorption and secondarily with chemoreception.

From the present studies it has also been shown that these sensilla are extremely sensitive to even minute mechanical stimuli and are capable of sensing the substratum. It appears that the pectines are concerned in the perception of

ground vibrations and are used more in warning of danger than in the detection of prey. The sense of olfaction exhibited by these sensilla is visualised to play a role in courtship and mating behaviour of the scorpion (Gopala Krishna Reddy 1967).

The vibration receptors are all the more important in the scorpions with nocturnal life. Much of the information they receive about the outside world is from the vibrations. In the capture of food and in defence and offence vibration is an important stimulus. The wide frequency range for which the scorpion is sensitive allows it to obtain information about the activities of several organisms which produce ground borne vibrations within this range. The presence of vibration receptors capable of responding to two separate frequency ranges being located at different places on the same leg is a unique phenomena worthy of further investigation. The food of the scorpions consists of insects, spiders, slugs, snails, toads, and some time even small mammals such as mice. It is possible that the high frequency vibration receptor present at the base of the claw might help in locating the faint crawling movements of some of these animals. The slit sense organ which might also respond to the air borne sound vibrations might be capable of perceiving the buzz of many insects.

Since this study is first of its type in scorpion, H.fulvipes and also of preliminary in nature, several crucial questions are open for further investigation. It is left for

enquiry as to what kind of sounds or vibrations the scorpions are exposed normally and to what extent scorpions with intact legs can detect the periodic motion or vibration in their environment and which parameters of the waves are detected by them.

Thus there are several other vital problems in scorpion H.fulvipes awaiting further clarification. Yet from the known facts it can be safely concluded that the scorpion has activities in a limited arena when compared with several insects. Accordingly the sensory structures are designed to cater the needs of the limited activities in the scorpions. The chemosensory hairs (type a) could discriminate only fewer number of chemical compounds if they are present in higher concentrations only unlike in many insects. The construction of the eye permits only to discriminate the intensities of the light but not to form any images of the objects (Ramakrishna 1963) unlike in many insects. But the scorpions seem to respond promptly to the most vital activities in self preservation. They have relatively well developed organs for food catching. They have relatively well developed organs for absorbing moisture most essential for metabolic activities. They have structures for olfaction to play an essential role in courtship. Finally the vibration receptors always alert the animal from the impending dangers from the predators. But the curiosity is all these sensory functions are delegated to the limbs unlike in the more evolved organisms.

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